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Studies on the flora of northern South America—XI.¹

New or noteworthy monocotyledons from British Guiana

H. A. GLEASON

The genus *Carludovica* contains at least thirty, and probably a good many more, species of tropical America. They are either acaulescent and palm-like in aspect, or climbers with palm-like leaves, and have a very characteristic and unusual type of flower-structure. The genus dates back to Ruiz and Pavon, who gave in 1798 only the briefest mention of the structural features of the flower, and not enough to enable one to relate their species to modern groups, except in the case of the economic species *C. palmata*. In 1807 Persoon, objecting to the length of the name, changed it to *Ludovia* and transferred the original five species. Oersted in 1857 proposed the genera *Sarcinanthus* and *Evodianthus*, described them well, and later gave excellent illustrations. Only one species has been associated with the former name and but three with the latter. They were merged with *Carludovica* by Bentham and Hooker, but kept separate by Drude in the *Pflanzenfamilien*. Brongnart in 1861 based a new genus on a Guiana plant and gave it the name *Ludovia*, since Persoon's *Ludovia* had never come into use. Drude founded a fifth genus *Stelostylis*, with one species, in 1881.

In the meantime numerous species had been described under the broad generic concept of *Carludovica*, and in probably half of them the structure of the flowers was not mentioned, or was stated in the most general terms; many of the species were based on completely sterile material, or on living plants in ornamental collections, the identity of which is notoriously easily lost. As a result, of about sixty species of *Carludovica* which have been proposed, at least half are little better than *nomina nuda*.

¹ Contributions from the New York Botanical Garden, No. 305.

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The omission of observation of flower-structure by so many botanists is difficult to account for. Poiteau, as early as 1822, gave a description and illustration of one species, the structure of which is so remarkable that it should have excited every contemporary to verify it and to confirm it among other species. Hooker gave excellent plates of species built on a plan so difficult that it is strange that they escaped segregation as genera. Yet Drude in the *Flora Brasiliensis* mentions the structure of the staminate flower in only three species out of fourteen, and a few years later described the genus in the *Pflanzenfamilien* in the most general terms only.

Material from British Guiana shows six general types of flower-structure, each sufficiently different to be ranked as a genus, as indeed two of them have. It seems better, however, to keep them in all in *Carludovica* as sections, where they are just as valuable, or more so in our present lack of knowledge of so many other species. If several new genera are to be segregated, there will be little left of *Carludovica* except the Panama-hat plant and its allies, and the remaining species can seldom be assigned with any degree of accuracy to a new genus because of lack of proper material for study.

These six subgeneric groups include eight species in British Guiana; others occur in Trinidad, Surinam, and French Guiana, representing in some cases still other subgenera. The association of these eight species with any of the sixty already described is very difficult and has been accomplished in only two cases. The subgeneric characters are presented in the key:

Receptacle of the staminate flowers flat or concave, the pedicel attached excentrically, distinctly asymmetric, the adaxial side more or less truncate, the remainder of the margin with 5-8 spreading lobes; stamens 5-12, on the upper surface, mostly marginal; spathes 2 or 3, all at the summit of the peduncle, the outer one or two lanceolate to ovate, the innermost enclosing the spike before anthesis and abruptly contracted above into a linear cusp; small or delicate acaulescent plants with spadices 1-2 cm. long.....Section I.

Receptacle of the staminate flowers funnellform or deeply concave, bearing the numerous (25-50) stamens on the inner surface; perianth-lobes 10 or more, symmetrically disposed around the margin.

Perianth-segments erect, somewhat enlarged distally, terete or radially flattened, hollow, imbricate in two series of which the outer is the smaller, with short, acute, distinctly inflexed tips; spathes 3 or 4, all above the middle of the peduncle.....Section II.

Perianth-segments tangentially flattened, rather thick and fleshy, regularly imbricate in one series.

Sepals of the pistillate flower short-triangular, equaling the sessile stigmas, all about equal in size; perianth-segments of the staminate flower about 12, more than 1 mm. wide, decurrent on the outside of the receptacle; stamens about 50-60, linear-oblong, 1.2-3 mm. long; spathes scattered, 8-10.....Section III.

Sepals of the pistillate flower rhomboid, one opposite pair twice as wide as the other, erect; style elongate, stoutly pyramidal, 3 mm. long, the cruciform stigmas not wider; perianth-segments of the staminate flowers minute, not decurrent; stamens about 25, short-oblong or almost square, about 0.5 mm. long; spathes 3, near the middle of the peduncle, the spadix stipitate.....Section IV.

Receptacle of the staminate flowers flat or nearly so, the pedicel expanded above into a solid obconic flat-topped receptacle, bearing the numerous stamens scattered over its surface; perianth-lobes marginal, small, in one or two series or none.

Receptacle of the staminate flowers nearly or quite symmetrical; filaments waxy-white, strongly swollen and subglobose at base.....Section V.

Receptacle asymmetric, the abaxial side with 4-7 large semi-globose submarginal yellow glands; perianth-lobes none; filaments slender.....Section VI.

SECTION I. Herbaria contain other specimens which greatly resemble the three following in general aspect and which doubtless belong also to this section.

Receptacle of the staminate flowers flat or nearly so, its lobes 4-10, those on the abaxial side linear or narrowly triangular; filaments very short and stout, or the anthers essentially sessile, with widely divergent pollen-sacs.

Filaments 0.2 mm. long; perianth-lobes finger-shaped, obtuse; stamens 4-9.....*C. pygmaea*.

Filaments none; perianth-lobes narrowly triangular, acute; stamens 12.....*insularis*.

Receptacle of the staminate flowers somewhat concave, or becoming flattened with age, its lobes about 8, short, obtuse; stamens 12; filaments short but very slender; pollen-sacs parallel and approximate. *C. nana*.

Carludovica pygmaea n. sp. Terrestrial, the leaves crowded on a short caudex about 5 cm. high; petioles slender, 6–10 cm. long, somewhat expanded below, mingled with linear sheaths 4–5 cm. long; leaf-blades 11–18 cm. long, bipartite for four fifths of their length, with a single common midrib, the segments linear-lanceolate, 10–13 mm. wide, long-acuminate; peduncles slender, several on each caudex, terete, about 7 mm. long; spathes 2, apical, the lower triangular, 20–25 mm. long, 7–10 mm. wide near the base, gradually tapering into a long slender tip, the upper enclosing the spadix before anthesis, its body subrotund, abruptly contracted distally into a linear cusp 5–7 mm. long; spadix 10–15 mm. long; pistillate flowers sessile, the 4 perianth-segments depressed-ovate, nearly concealed, bearing filiform staminodes; stigma cruciform, sessile, each lobe obovate; staminate flowers on short flattened pedicels; receptacle abruptly expanded, flat, somewhat circular, inequilateral, 1.8–2.3 mm. wide, truncate along the smaller adaxial side, elsewhere bearing 5–9 obtuse, finger-shaped lobes 0.4–0.6 mm. long; stamens 1 central and 3–8 near the margin; filaments very stout, 0.2 mm. long, prolonged into the stout connective so that the oblong pollen-sacs (0.6 mm. long) become widely divergent at base.

Type, *Hitchcock 17,388*, collected in forest at Tumatumari, British Guiana, 3–5 Jan. 1920, and deposited in the herbarium of the New York Botanical Garden.

Carludovica insularis n. sp. Plants larger and stouter than the preceding; terrestrial; petioles as much as 35 cm. long; leaf-blades 50 cm. long, bipartite for three fifths of their length, with a single common midrib, the segments 5 cm. wide, not notably acuminate; peduncles slender, as much as 3 dm. long, mingled below with linear sheaths; spathes 2, apical, the outer 8 cm. long, ovate-lanceolate below, narrowed above into a linear cusp 5 cm. long, the inner broadly ovate-rotund, closely enveloping the spike before anthesis, abruptly narrowed into a short linear cusp 8 mm. long; spadix 15–20 mm. long; pedicel of the staminate flowers flattened, abruptly dilated into a flat receptacle, the latter somewhat pentagonal in shape, about 3.5 mm. in diameter, truncate on the narrower side, elsewhere irregularly 7–9-lobed, the lobes triangular-linear, acute, 1–1.5 mm. long; stamens 12, some central, the majority near the margin or even on the ends of the lobes; anthers sessile by a

broad base, the pollen-sacs oblong, 0.5–0.6 mm. long, approximate above, widely divergent below.

Type *Broadway 4066*, collected in woods, Tobago, British West Indies, 30 Sep. 1911, and deposited in the herbarium of the Royal Botanic Gardens in Kew. A second sheet, purporting to be the same collection, has a huge leaf with 3 midribs, irregularly lobed above. It is very doubtful if it actually belongs here. Another Tobago sheet of the species, collected two years later, is much smaller in every way, the petioles and peduncles about 1 dm. long and the blades 17–21 cm. long.

Carludovica nana n. sp. Acaulescent, terrestrial; petioles dilated at base, slender, 17–25 cm. long, more or less mingled with linear sheaths; leaf-blades 15–20 cm. long, bipartite for four fifths of their length, with a single common midrib, the segments 15–20 mm. wide, slenderly acuminate; peduncles slender, about 2 dm. long; spathes 3, apical, the two outer lanceolate, 5 and 4 cm. long, slenderly acuminate, the inner broadly ovate at base, closely enfolding the spike, abruptly narrowed to a cusp 8 mm. long; spadix 15 mm. long; staminate receptacle broadly and shallowly funnel-form, becoming somewhat explanate in age, about 1.5 mm. in diameter, asymmetric, the narrower side truncate, the remainder of the margin bearing about 8 short, obtuse, irregular lobes; stamens 12, mostly near the margin, the pollen-sacs broadly oblong, 0.4–0.6 mm. long, parallel and opposite on very slender filaments 0.4 mm. long.

Type collected by *R. H. Schomburgk*, without number, in stony beds of rivers and brooks in the Serra Mey, British Guiana, and deposited in the herbarium of the Royal Botanic Gardens at Kew.

SECTION II. Only one species has been described in such terms that it can be authentically referred to this section, *C. funifera* (Poit.) Kunth, a plant of French Guiana, with leaves which are bifurcate only in the distal third, according to Poiteau. To this we now add a second:

Carludovica coronata n. sp. Stems stout, climbing to a height of 15 m.; petioles 15–30 cm. long, sheathing at base, channeled on the upper side; leaf-blades 3.5–6.5 dm. long, bifurcate for two thirds to four fifths of their length, or rarely less, with a single common midrib, the segments many-veined, acuminate, 25–50 mm. wide; peduncles 15–20 cm. long; spathes 2–4, at or near the summit, ovate to ovate-lanceolate, acumi-

nate, soon deciduous, exceeding the spike; spadix 3–5 cm. long; staminate flowers obconic on a short pedicel, about 4 mm. in diameter, perianth-lobes about 20, biseriate, terete or slightly flattened radially, hollow, rounded on the top, the actual tip acute and inflexed, the inner series somewhat obovoid, the outer similar but smaller; stamens about 24, in two circles of about 12 each, on the inside of the deeply concave receptacle; anthers oblong, 0.6 mm. long, about equaling the slender filaments.

Type, *De La Cruz 4444*, collected at Kaieteur Falls, British Guiana, 23 Oct.–3 Nov. 1923, and deposited in the herbarium of the New York Botanical Garden. The species is widely distributed through British Guiana, and is represented at Kew or New York by *Appun 259*, *Jenman 736*, *1317*, *Hitchcock 16,988*, *Gleason 150*, *De La Cruz 1445*, *1934*, *3285*, and the type.

SECTION III. The manuscript name of *C. sarmentosa* was applied by Sagot to a specimen from French Guiana, but was never published by him. Drude published it for Sagot, citing only Brazilian material and possibly drawing his description from that rather than from the Guiana plant. A specimen at Kew of the original collection enables us to refer the species to this group.

Spathes broadly rotund to subcordate at base.....*C. sarmentosa*.
Spathes narrowed to the base.....*C. bracteosa*.

***Carludovica bracteosa* n. sp.** Stems climbing; petioles about 1 dm. long, flattened or channeled above; leaf-blades tripartite for about two thirds of their length, inequilateral, the single midrib running to one sinus, the single segment 2–3 cm. shorter at base than the double segment, all segments 3–5 cm. wide, acuminate, 7–10 costate, somewhat plicate; peduncles stout, 15 cm. long; spathes about 10, evenly distributed, the lowest lanceolate, 2 cm. long, the upper enlarged, linear-oblong, 8–10 cm. long, acute, narrowed to the base; spike ovoid, 4–5 cm. long; perianth-segments of the pistillate flowers erect, triangular, acute, 3 mm. long and wide, equaling the cruciform stigmas; staminodes about 3 cm. long; staminate flowers campanulate, on a pedicel 3.5 mm. long, the hollow interior 2.7 mm. deep; perianth segments 12, 3 mm. long, only the distal 1 mm. free, the whole segment linear-oblong, decurrent on the receptacle, contiguous below, abruptly dilated at the free tip to 1.5–1.7 mm. wide and half overlapping with adjacent segments, rounded or barely retuse at the fleshy pinkish tip;

stamens about 60, covering the inside of the flower; filaments slender, 0.8 mm. long; anthers erect, linear-oblong, the central 2.7 mm., the others progressively reduced to 1.2 mm. long.

Type, *De La Cruz 1505*, collected at Dadanawa, British Guiana, 14 June 1922, and deposited in the herbarium of the New York Botanical Garden; a second sheet is *De La Cruz 1309*.

C. Kegeliiana Lem., described as having ten spathes, may also belong to this section.

SECTION IV. *Stelostylis* (Drude, as genus). The essential feature of Drude's genus is the elongate style, but it may be distinguished, at least from Guiana species, equally well by staminate structures. The following differs from Drude's *Stelostylis coriacea* in its long petioles and peduncles, prominently veined leaves, and 25 stamens.

Carludovica stylaris n. sp. Petioles 6 dm. long; leaf-blades 7 dm. long, bifurcate for three fourths of their length, with a single common midrib, the segments 6 cm. wide, abruptly acuminate, prominently 7-8-nerved; peduncles 2-2.5 dm. long, stout, slightly angular, invested at base by 2-3 elliptical obtuse or acute sheaths 4-5 cm. long; spathes apparently 3, the lower somewhat beyond the middle, the upper 2-3 cm. below the spike, narrowly lanceolate, 8 cm. long; spadix becoming 5 cm. long at maturity; perianth-segments of the pistillate flowers thick and woody, 3 mm. long, 1.5 or 3 mm. wide, obtuse; style stout, pyramidal, 4-angled, 3 mm. long, the cruciform stigmas 2 mm. in expanse; staminate flowers funnellform or obconic, 2 mm. long, fleshy, the receptacle concave within; perianth-segments about 12, erect with recurved margins, semi-circular, fleshy and rounded, 0.3 mm. long, 0.4-0.6 mm. wide; stamens about 25, covering the receptacle; anthers nearly square, 0.5 mm. long, flattened tangentially, on slender filaments 0.2 mm. long.

Type, *Jenman 898*, collected on trunks of trees and rocks, in forests near the Kaieteur savanna, British Guiana, Sep.-Oct., 1881, and deposited in the herbarium of the Royal Botanic Gardens at Kew. Field notes state that the stem is two inches thick and not climbing.

SECTION V. *Sarcinanthus* (Oersted, as genus). A sheet of *Jenman 900*, from British Guiana, matches nicely with the type collection of *Carludovica latifrons* Drude and is referred to

that species, while its flower structure shows clearly that it is related to Oersted's species and to the few others that have elsewhere been described with similar characters.

SECTION VI. I know of no other published species with which the following may be compared.

Carludovica glandulosa n. sp. Terrestrial, acaulescent; petioles slender, 4 dm. long, channeled and wing-margined throughout, very gradually expanded into the blade; leaf-blade about 11 dm. long, bifurcate, the segments 14 cm. wide, acuminate, many-veined; peduncles 8-10 cm. long, bearing above the middle 3 ovate-oblong, sessile and clasping, acuminate spathes 5-6 cm. long; spadix on a stalk 1 cm. long, ellipsoid or cylindric, 25-30 mm. long; staminate flowers woody, asymmetric, flat on top, 2.2 mm. in diameter, obconic; perianth-segments none; receptacle bearing on the outer side, just below the margin, 4-7 semiglobose yellow glands, the largest 0.6 mm. in diameter, the smaller ones at the ends of the row half as large; stamens about 25; anthers oblong, 0.6 mm. long by 0.4 mm. wide, on slender filaments 0.2 mm. long.

The type is *Jenman 2105*, collected in the Mt. Russell District, British Guiana, and deposited in the herbarium of the Royal Botanic Gardens at Kew.

Anthurium expansum n. sp. Section *Schizoplacium*: epiphytic, probably scandent, the stem stout and thick; leaf-blades ample, thinly membranous, 7-parted; central three lobes separate to the base, elliptic-oblong, 35-40 cm. long by 12 cm. wide, gradually narrowed above to a slender cusp 2 cm. long, long-cuneate below to a sessile base; two lateral lobes on each side connate for about 8 cm. above the inequilaterally cuneate base, the inner lobe narrowly elliptic-oblong, 35 cm. long, 8 cm. wide, the outer lobe falcate-lanceolate, 28 cm. long by 4.5 cm. wide, inequilateral at base and slenderly acuminate; costae elevated on both sides, the lateral veins 8-12 mm. apart, plane or somewhat depressed above, prominulous beneath, ascending at an angle of 50-60° and confluent into a collective nerve 2-3 mm. from the margin; peduncle at least 3 dm. long; spadix narrowly conical, 15 cm. long; spathe linear-lanceolate, equaling the spadix.

Type, *Lang 223*, collected at Kurupung, Mazaruni River, British Guiana, 23 Nov. 1922, and deposited in the herbarium of the New York Botanical Garden. *Anthurium expansum* appears to be most closely related to *A. Andersonii* Schott,

and differs in its much larger, 7-parted leaves with elliptic lobes, in its submarginal collective nerve, and in its larger spathe and spadix.

Anthurium glaucophyllum n. sp. The name is proposed to cover a plant from British Guiana, cultivated at Kew, where it flowered in October, 1891, and where type material is conserved in the herbarium. Petioles slender, 4 dm. long; leaf-blades oblong-lanceolate, thin but firm, 5 dm. long, 13 cm. wide, acute, broadly rounded at base, very glaucous beneath; lateral veins numerous, 1-2 cm. apart, ascending at an angle of 60° , veinlets prominent beneath, conspicuously reticulate above; collective nerve prominent, about 1 cm. from the margin; peduncle slender, 5 dm. long; spathe narrowly ovate-oblong, 4 cm. long, erect, equaling the slender spadix.

Anthurium potarense n. sp. Section *Semaeophyllum*; stem not known; petiole slender, 3-4 mm. in diameter, subterete, channeled on the upper side, 4-5 dm. long (or more); blades firm in texture, drying brownish green, deeply 5-lobed, the central three lobes narrowly obovate-oblong, 7-11 cm. wide, 32-40 cm. long, gradually tapering to an abruptly acuminate tip, long-cuneate at base, the outermost lobes narrowly oblong, 27-30 cm. long, 5-6 cm. wide, acuminate, connate with the interior lobes for 1-2 cm., equilateral except for a semicircular basal lobe about 6 cm. in diameter; lateral veins prominent, arising at an angle of about 75° , slightly arcuate and confluent into a collective nerve 3-5 mm. from the margin; veinlets prominently reticulate; peduncle at least 2 dm. long; spathe narrowly lanceolate, about equaling the spadix, which is slenderly cylindric, 10 cm. long.

Type, *Jenman 7466*, collected on the Potaro River, British Guiana, Oct. 1898, and deposited in the herbarium of the Royal Botanic Gardens at Kew. *A. potarense* seems to be most closely related to *A. fissum* C. Koch, but the leaves are much more deeply lobed.

Anthurium obovatum n. sp. Stems elongate, climbing by rootlets, 2 cm. in diameter, the internodes 3-5 cm. long; petioles 6-7 dm. long, winged along the upper side for 15 cm. at the base, the remainder slender, channeled above; leaf-blades 7-parted, rather thin but firm; middle 3 segments distinct to the base, obovate, 4-4.5 dm. long, 16-17 cm. wide, abruptly rounded above to a falcate apiculum 1 cm. long, narrowed below the middle to a long-cuneate, petiole-like, winged base; lateral veins 10-20 mm. apart, ascending at an angle of 60° and very slightly arcuate, connected by a collective nerve about 5 mm.

from the margin, elevated on both surfaces; veinlets prominulous beneath and conspicuously reticulate; fourth and fifth segments resembling the preceding and only slightly smaller, their base more broadly winged and connate with the outermost segments for 4 cm. above the base, their midribs not confluent; outermost segments narrowly obovate, 35 cm. long, 12 cm. wide, apiculate, the inner margin long-cuneate below to the point of confluence with the inner segment, the outer margin with a thumb-like basal projection, its free limb oblong, apiculate, 10 cm. long above the narrow sinus, 6 cm. wide, traversed by the usual collective nerve and by a costa which leaves the midvein of the segment 6 cm. above its base and is denuded on the outer side for 8-9 cm. above the summit of the petiole, its outer margin broadly rounded below to a cuneate base; peduncle stout, 3 dm. long, oval in section; spathe linear-oblong, 2 dm. long, 3 cm. wide, apiculate, conspicuously veined; spadix stout, purple, 2 dm. long, 2 cm. in diameter as pressed.

Type, *Altson 475*, on tree trunks in the forest, Anandabaru, Kopinang River, British Guiana, April, 1926, deposited in the herbarium of the Royal Botanic Gardens at Kew. It is a member of the section *Schizoplacium* and differs from the related species in the size of the spathe and spadix and the characters of the leaf.

Dieffenbachia paludicola N. E. Brown. Perhaps stemless; petiole 20 cm. or more long, and in the dried specimen 2 cm. thick; blade cuneately oblanceolate, acute, uniformly green, about 75 cm. long and 18 cm. broad at about 25 cm. below the apex, thence gradually narrowing into the petiole; midrib stout; primary lateral veins about 12, curved, ascending; peduncle about 30 cm. long, and in parts of the dried specimen 8 mm. thick, so probably much stouter when alive; spathe about 32 cm. long and in the dried state about 2 cm. in diameter, shortly acute at the apex, apparently green; adnate part of the spadix about two-thirds as long as the spathe, with the fertile and barren flowers laxly scattered along it; ovary 2-3-celled; male part of the spadix not seen.

British Guiana: in a swamp near the Penal Settlement, *Hitchcock 17030* (type in herb. New York Botanical Garden). In all probability *Jenman 5771* is the same species, but the specimen at Kew is too imperfect to decide, only the upper part of the leaf being represented. It was collected on the Essequibo River and is stated to be 'acaulescent, gregarious in water in forests, no clear petiole.'

Philodendron demerarae n. sp. Stems acaulescent, epiphytic; petioles stout, not winged, 3–6 dm. long, 1 cm. wide or less when pressed; leaf-blades cordate-sagittate, the margin at the base distinctly ascending from the summit of the petiole to form a broadly cuneate base, thence at once spreading or somewhat recurved into the basal lobes, which are semi-circular or depressed ovate, broadly rounded, and somewhat divergent; terminal lobe triangular-ovate, somewhat longer than broad, acute to abruptly acuminate; lateral veins from the midvein 12–18 on each side, the upper straight and ascending at an angle of about 60°, the lower 3–5 approximate at base, spreading at right angles or recurved and gradually diverging in the basal lobes, the lowest veins not naked in the sinus; lateral veins of the second rank fine, closely parallel, about 1 mm. apart; peduncle apparently 5 cm. long, slender; spathe 7–10 cm. long, purple at base, white above, closely convolute below; spadix about 7 cm. long, of which the basal fourth is pistillate and scarcely swollen, and the terminal two-thirds is staminate; ovules numerous in a vertical row in each loculus.

Type, *Hitchcock* 16,987, collected on trees in wet forest southeast of Lamaha Stop-Off, British Guiana, Nov. 27, 1919, and deposited in the herbarium of the New York Botanical Garden. Other sheets referred here are *Jenman* 5759 from the Essequibo River and *Gleason* 121 from Tumatumari. The leaves measure 32, 42, and 44 cm. along the midvein of the terminal lobe by 23, 35, and 41 cm. wide.

Philodendron platypodum n. sp. Stem slender, climbing, the internodes 2–3 cm. long; petioles stout, 8–10 cm. long, broadly winged to the summit, 15 mm. wide at base, 10 mm. at the rounded apex; leaf-blades firm in texture, elliptic, distinctly inequilateral, 21–23 cm. long, 9.5–11 cm. wide, abruptly narrowed above to a cusp 1 cm. long, broadly rounded at base; principal lateral veins 6–9 on each side, ascending at an angle of 70°, scarcely more prominent than the secondary, which are 1 mm. apart; peduncle stout, 2.5 cm. long; spathe 12 cm. long, green within and without, closely convolute at base, not obviously constricted, partially expanded and cuspidate above; spadix 13 cm. long.

Type, *Jenman* 5762, collected at Lama, British Guiana, Apr. 1889, and conserved in the Jenman Herbarium. The species is a member of the section *Pteromischum*, and finds its nearest relative in *P. cannifolium* (Rudge) Engler, which differs in its narrower, thinner leaves, cuneate to the base and more distinctly acuminate, and in its cream-colored, spotted spathe.

Philodendron subsessile n. sp. Stems slender, climbing, the flexuous internodes 2.5–5 cm. long, the nodes marked by lanceolate cataphylls 2 cm. long; petioles slender, wingless, 5–15 mm. long; leaf-blades thin, dark green, cordate-ovate, 5–9 cm. long, 3–7 cm. wide, abruptly acuminate into a short filiform cusp 1–2 mm. long, the basal lobes rounded, separated by a narrow sinus about equaling the petiole; lateral veins about 6 on each side, poorly developed, more or less approximate toward the base of the leaf.

Type, *Gleason 460*, collected in dense forest at Tumatumari, British Guiana, 18 June–8 July 1921, and deposited in the herbarium of the New York Botanical Garden. Other specimens from Guiana are *Gleason 461*, *De La Cruz 1029*, and *De La Cruz 3708*. These all have smaller and proportionately narrower leaves, but differ from the type in no essential respect.

Philodendron dioscoreoides n. sp. Stems slender, climbing, the comparatively straight internodes 5–7 cm. long; cataphylls at the nodes apparently none; petioles 3–6 cm. long, nearly equaling the blade, conspicuously winged on the basal half or nearly to the summit; leaf-blades narrowly cordate-ovate, 6–9 cm. long, 4–6 cm. wide, acuminate into a slender cusp 2–3 mm. wide and about 1 cm. long, often falcate, the basal lobes rounded, separated by a broad shallow sinus; principal lateral veins poorly developed, about 6 on each side.

Type, *Gleason 459*, collected in dense forest at Tumatumari, British Guiana, 18 June–8 July 1921, and deposited in the herbarium of the New York Botanical Garden. Other specimens are *Bartlett 8125* and *Gleason 449*, both of which have smaller leaves than the type.

P. subsessile and *P. dioscoreoides* both represent sterile species, possibly juvenile, or possibly sterile because of some environmental deficiency. Both were common in the forest at Tumatumari, but repeated search failed to reveal any connection between either of them and other fertile species. Both are related to *P. micans*.

Rhodospatha venosa n. sp. Stem high-climbing, with both aerial and hold-fast roots, woody, the internodes about 12 cm. long by 1 cm. in diameter; petioles slender, vaginate to the geniculus, which is 15 mm. long; blades membranous, green on both sides, ovate-oblong, 33 cm. long by half as wide, abruptly acute, rounded at base; principal lateral veins 1 cm. apart, scarcely more prominent than the secondary (1–1.5 mm.

apart), ascending at an angle of $45-60^{\circ}$; leaves on the peduncle 3, bladeless, strongly vaginate, narrowly linear, 13 cm. long, borne 6 cm. below the summit; spathe not seen; spadix cylindrical, obtuse, 8 cm. long, on a stipe 1 cm. long; flowers all perfect.

Type, *Gleason 153*, from dense upland forest, Tumatumari, British Guiana, in the herbarium of the New York Botanical Garden. It is apparently related to *R. Melinoni* (Engl.) Engl. and Krause, in which the leaf is glaucous beneath, with the veins leaving the midrib almost at right angles.

Syngonium connatum n. sp. Leaf-blades conspicuously bluish-green above, dull green beneath, deeply 3-parted; terminal segment elliptic to rhombic-elliptic, 25-40 cm. long, 13-15 cm. wide, abruptly short-acuminate, equilateral, narrowed to a broadly sessile base; lateral segments ovate, 20-30 cm. long, 9-14 cm. wide, acute, strongly inequilateral or somewhat falcate, the upper side two-thirds as wide as the lower, concavely cuneate at base into a wing 1 cm. wide confluent with the central segment, the lower side broadly rounded or subcordate to an abruptly cuneate base, the stalk naked for 15-20 mm.; all lateral veins nearly parallel, straight or slightly arcuate below, curved forward near the margin, and finally confluent, but without forming a definite collective nerve.

Type, *Jenman 5756*, collected along the Rupununi River, British Guiana, Oct. 1889, and deposited in the herbarium of the Royal Botanic Gardens at Kew. Only the leaf-blades are available on the three sheets examined. The great size, bluish or glaucous tint, and broadly winged base of the lateral leaflets distinguish it from all other species seen by me.

Syngonium ternatum n. sp. Stems climbing, juice milky; petioles about 3 dm. long, conspicuously wing-margined for about half their length; leaf-blades membranous, bright green, trifoliate; terminal segment nearly sessile, equilateral, oblong, 17-18 cm. long, 6-7 cm. wide, obtuse, narrowed to the base, the lateral veins ascending irregularly at an angle of about 45° , united into an obscure collective nerve about 8 mm. from the margin; lateral segments elliptic, inequilateral or somewhat falcate, as long as the terminal, obtuse or subacute, the inner half cuneate to an acute base, the outer half narrowed to an obtuse or slightly cordate base; stalks of the lateral segments 10-15 mm. long, naked on the basal side, very narrowly winged on the distal; peduncles axillary, about 1 dm. long, clavate above; spathes and spadix not seen; the syncarpous berry yellow, 3 cm. long.

Type, *De La Cruz 1288*, collected along the Waini River, British Guiana, 6 Feb. 1922, and deposited in the herbarium of the New York Botanical Garden. *De La Cruz 1469*, from the upper Rupununi River, is also referred here: it has leaves 22 cm. long, the lower half of the lateral segments subcordate at base, and a fruit with about 10 carpels. The species most nearly resembles *S. yurimaguense* Engl. from Peru, which has smaller and proportionately narrower leaflets with a rather prominent basal lobe, and petioles winged for three-fourths of their length.

Paepalanthus Jenmani n. sp. Caudex very short, thinly lanate; leaves densely cespitose, soft and lax, erect, narrowly linear, 1–2 mm. wide, 8–12 mm. long, glabrous, subulate-tipped; peduncles 20–25 cm. tall, roundly 3-costate, glabrous, twisted, their sheaths strongly twisted, sparsely hirsute, 4–5 cm. long, with long-oblique orifice and subscarious lamina; heads hemispheric, 3–5 mm. wide; involucre bracts broadly ovate to ovate-oblong, appressed, regularly imbricate in several series, glabrous; receptacle hairy; staminate flowers: pedicel very slender, glabrous, 1.3–1.7 mm. long; perianth hyaline; sepals free, glabrous, elliptic-obovate, obtuse, 1.7 mm. long; petals free, narrowly obovate, 2 mm. long, obtuse or rounded at apex, glabrous; stamens 3, inserted on the very base of the corolla, opposite the petals, about equaling the sepals, the filaments slender, the anthers 2-locular; pistillate flowers sessile; sepals free, elliptic, 1.5 mm. long, obtuse, glabrous; petals subulate-spatulate, erect and closely appressed to the pistil, 2.3 mm. long, 0.1–0.2 mm. wide, densely hirsute throughout with erect hairs; staminodes none; ovary glabrous, thick-fusiform 0.5–0.6 mm. long; style very short; stigmas 3, filiform, simple; appendages 3, inserted at base of stigmas, erect, narrowly clavate, just equaling the stigmas.

Type, *Jenman 1032*, collected on the Kaieteur savanna, British Guiana, Sep.–Oct. 1881, and deposited in the herbarium of the Royal Botanic Gardens at Kew. It is most closely related to *P. capillaceus* Klotzsch, from which it may be distinguished by its wider leaves and narrower, densely hirsute petals in the pistillate flowers.

Syngonanthus brevifolius n. sp. Stems tufted, freely branched, 3–5 cm. long, somewhat lanate, leafy in the terminal centimeter; leaves crowded, recurved or spreading, narrowly lanceolate, 4–6 mm. long, 1 mm. wide, glabrous, prominently nerved; peduncles solitary in some of the upper axils, 10–16

mm. long, slender, 3-angled, somewhat twisted, sparsely hirtellous and occasionally glandular; sheaths ample, 3-4 mm. long, glabrous, obliquely truncate at the summit to form an obtuse lamina 1.2 mm. long; heads 2-3 mm. in diameter; outer bracts about 5, broadly oblong-elliptic, 1.1-1.5 mm. long, 0.9-1.1 mm. wide, glabrous or nearly so, membranous, rounded at apex; inner bracts oblong, obtuse, 1.2 mm. long by 0.5 mm. wide, glabrous; pistillate flowers: pedicel 0.7 mm. long, hirsute; sepals scarious, obovate-oblong, symmetrical, 1.0 mm. long by 0.5 mm. wide, rounded at apex, glabrous; petals separate, scarious, spatulate-obovate, 1.2 mm. long, 0.5 mm. wide, glabrous, rounded at the apex; style 0.2 mm. long, bearing 3 simple stigmas without appendages; staminate flowers: sepals scarious, cuneate-obovate, 1.0 mm. long, 0.4 mm. wide, glabrous, rounded at apex; petals connate into a broadly obconic tube 0.7 mm. long, not involute, crowned with 3 lobes 0.15 mm. long; stamens exerted.

The type is *Jenman 4755*, collected at Bartica, British Guiana, Nov. 1888, and deposited in the herbarium of the Royal Botanic Gardens at Kew. *S. brevifolius* is related to *S. anomalus* Ruhl., but differs in its much shorter leaves, with firm texture and prominent nerves, and its shorter, glabrous, truncate peduncular sheaths with obtuse lamina.

***Syngonanthus longipes* n. sp.** Caudex short and stout, woolly; basal leaves densely cespitose, firm or rigid, ensiform-linear, 6-9 cm. long, 3-6 mm. wide, obtuse, glabrous, the nerves about 9, prominent beneath; flowering branch single, 2-3 dm. long, terete, glabrous; involucreal leaves resembling the basal, numerous, acute; peduncles 4-14, each 2-4 dm. long, somewhat twisted, costate, glabrous, their sheaths obliquely cleft, multi-steriate, acute; heads subglobose, 4-6 mm. wide; outermost bracts nearly rotund, the middle ones broadly obovate, the inner oblong-obovate, all glabrous, rounded at apex, ranging from 1.7 mm. long and 1.4 mm. wide to 2.3 mm. long by 1.2 mm. wide; subtending bracts narrowly obovate-oblong, 2.2 mm. long, just equaling the flowers; staminate flower: sepals obovate, 1.5 mm. long, 0.7 mm. wide, subacute, nearly glabrous; corolla tubular for 0.4 mm., campanulate above; pistillate flower: sepals narrowly obovate-oblong, 2.0 mm. long by 0.8 mm. (posterior) or 0.6 mm. (lateral) wide, obtuse, scarious at margin, nearly glabrous; petals 2 mm. long, densely hirsute, especially below, clearly separate at base, 0.4 mm. wide at the middle, connate above into a subulate, claw-like organ beyond the styles; ovary 0.7 mm. long; style, including appendages, 0.5 mm. long; stigmas filiform, about 1.0 mm. long.

Type, *Appun 1199*, from the Roraima district of British Guiana, in the herbarium of the Royal Botanic Gardens at Kew; other specimens are *Schomburgk 1060* and *Im Thurn 33*. The type was reported by Oliver as *Paepalanthus Schomburgkii* Klotzsch and this name is written on the Appun sheet but not on either of the two Schomburgk specimens. The descriptions of *P. Schomburgkii* do not agree with this plant in many important respects, nor do they cite any collection number.

Syngonanthus tricostatus n. sp. Leaves densely cespitose on a short caudex, ensiform-linear, thick, rigid, subcartilaginous with obtuse margins, 4–7 cm. long, 2–3 mm. wide, sharply acute, strongly twisted, many-nerved, glabrous, gradually dilated at base; peduncles solitary, 20–25 cm. high, strongly twisted, tricostate, glabrous, the sheath 35–65 mm. long, about equaling the leaves, oblique, sharply acute and subscarious at the apex; heads campanulate, 6–7 mm. high, the involucre 4 mm. high, conspicuously exceeded by the silvery flowers; bracts regularly imbricate, glabrous, broadly ovate-oblong, the exposed portion rotund, brown, obtuse or rounded, scarious at the margin; receptacle flat; staminate flowers: pedicels 2 mm. long; sepals separate, erect, scarious, narrowly oblong-elliptic, 2.7 mm. long by 0.5–0.6 mm. wide, glabrous, obtuse or subacute, the lateral slightly falcate; petals connate below for 1 mm. into a short, slightly funnelform tube, thence separate, erect, narrowly oblong-ovate, obtuse or subacute, scarious, glabrous, the free lobes 3 mm. long, 0.8 mm. wide; filaments filiform, anthers 2-theous; pistillate flowers: pedicels none; lateral sepals narrowly oblong, conspicuously falcate, 2.2 mm. long, acute; posterior sepal 2.6 mm. long, symmetrical, narrowly oblong-lanceolate, acute; all sepals hyaline and glabrous; petals 3.5 mm. long, strictly erect and connivent, narrowly spatulate, the hyaline glabrous blade closely involute and appearing subulate, lower fourth of the petal densely hirsute with erect brown hairs covering the whole claw; ovary sharply 3-angled.

Type, *R. H. Schomburgk*, first collection, without number, from the Roraima district in British Guiana, deposited in the herbarium of the Royal Botanic Gardens at Kew. It differs from *S. xeranthemoides* in its very thick, glabrous, subcartilaginous, obtuse-margined, strongly twisted, proportionately broader, actually shorter leaves, the longer peduncular sheaths, the smaller heads and the more scarious-margined bracts.

Abolboda rigida n. sp. Leaves cespitose, numerous, erect, 15–20 cm. long, 5–7 mm. wide, thick and rigid, prominently

dilated at base, pungent at apex; scapes 3, rather stout, glabrous, 6-8 dm. high; bracts a single opposite pair somewhat above the middle of the scape, loosely erect, broadly linear, sheathing and overlapping below, scarious-margined, tapering to the pungent tip, 3-5 cm. long; heads broadly ovoid or subglobose, 14-18 mm. long, many-flowered; involucre bracts firm, scarious at margin, finely veined, the outermost ovate, the inner gradually elongate; sepals 2, naviculate, carinate, oblong, 13 mm. long by 3 mm. wide as folded; corolla-tube slender, 13 mm. long, its lobes broadly round-obovate, 10 mm. long; filaments slender, nearly 5 mm. long; anthers 2 mm. long, prominently prolonged at base; ovary obovoid, 4 mm. long; style very slender, 15 mm. long, the two slender appendages attached 2 mm. from the base, 4 mm. long and abruptly recurved near the middle.

Type, *Schomburgk 146.5*, from British Guiana, in the herbarium of the Royal Botanic Gardens at Kew. It is most closely related to *A. poarchon* Seub., of which I have seen the type. The latter is a smaller, more slender plant with shorter and narrower leaves, somewhat narrower and more pointed involucre bracts, and narrower, conspicuously acuminate sepals.

Xyris cyperoides n. sp. Section *Nematopus*; caespitose, essentially acaulescent, the leaves at base more or less surrounding the scapes and often somewhat twisted and stemlike in aspect; leaf-blades filiform, 10-16 cm. long, 0.3-0.4 mm. wide by half as thick, the edges obtuse, the sides minutely scaberrate under a strong lens, gradually expanded below into a narrow scarious sheath; scapes about equaling the leaves, not flattened, several-ribbed; heads obovoid, becoming obconic under pressure, 3-4 mm. long; bracts erect or loosely appressed, becoming spreading when pressed, obscurely carinate, the outer most ovate-lanceolate, acute, the upper narrowly ovate, acuminate, only the uppermost one or two fertile; lateral sepals free, 3.5 mm. long, linear-spatulate, carinate, inequilateral, the narrower side firm and entire, the broader side hyaline and often lacerate near the middle, the keel entire; petals and stamens not seen; placentae basal.

Type, *Jenman 1056*, from Kaieteur savanna, British Guiana, Sep.-Oct., 1881, deposited in the herbarium of the Royal Botanic Gardens at Kew. It is a member of Malme's *Stirps X. guianensis*, and is most closely related to *X. subuniflora* Malme and *X. Grisebachii* Malme. From the former it differs in its long leaves and narrow sheaths.

Rapatea viscosa n. sp. Leaves all basal, linear, 2 m. long, the basal sheath flat, 3 dm. long, 25 mm. wide, the blade 4 cm. wide, narrowed to the base; peduncles stout, erect, 6-9 dm. high, strongly angled and dilated above; involucre of four bracts, at first erect, more or less connate, enclosing the heads, and covered with mucus, later separate and reflexed, brown, membranous or subscarios, the outer pair narrowly triangular, 10 cm. long, 30-35 mm. wide at the base, the inner linear-triangular, 4-7 cm. long, 1 cm. wide at base; heads semiglobose, 4 cm. in diameter, on a broadly conic, fleshy receptacle 15 mm. high; flowers sessile; bracts about 15, stiff, coriaceous, imbricate, ovate-lanceolate, acuminate to a short subulate tip, the largest 14 mm. long, the innermost slightly shorter; sepals lanceolate, bracteoid, long-acuminate, 12 mm. long.

Type, *Alison 388*, common among sandstone boulders, on top of the escarpment, Kurupung Mountains, British Guiana, 1 Sep. 1925, deposited in the herbarium of the Royal Botanic Gardens at Kew. It differs from the other three Guiana species in the presence of four bracts enclosing the sessile flowers.

Stegolepis angustata n. sp. Acaulescent herb; leaf-sheaths distichously imbricated at base, strongly folded longitudinally, firm or subcoriaceous, narrowly elliptic, 2-5 cm. wide, 15-20 cm. long, gradually narrowed to the acute apex, finely nerved; leaf-blades linear, 2-3 cm. wide, 6-8 dm. long, gradually acuminate to an obtuse tip, long-cuneate at base, finely many-nerved; scape axillary, apparently single, 8-12 dm. tall, slender, prominently angled below, somewhat quadrangular and flattened above; involucre none; heads 3-4 cm. in diameter, the flowers sessile, 15-17 mm. long; bracts pale brown, coriaceous, rigid, regularly imbricate in several series, obtuse, the outer short-ovate, the inner oblong; sepals ovate-lanceolate, acute, 15 mm. long; petals with sub-rotund blade, the claw-like bases somewhat connate; anthers linear-lanceolate, 4-locular, opening by a single oblique terminal pore; ovary 3-celled, the ovules several in each cell.

Type, *Jenman 958*, collected on the Kaieteur savanna, British Guiana, Sep.-Oct. 1881, and deposited in the herbarium of the Royal Botanic Gardens at Kew. It differs from *S. guianensis* Klotzsch, of Roraima, in its tapering sheaths, cuneate leaf-bases, and pale brown bracts; from *S. ferruginea* Baker, also of the Kaieteur region, in its tapering sheaths, pale brown bracts, solitary peduncles, and large flowers and heads.

Tofieldia rupestris n. sp. Leaves cespitose (not distichous), coriaceous, at the summit of a short stout rhizome, broadly

linear, erect and spreading, 4–9 mm. wide, 6–15 cm. long, long-acuminate, glabrous; scape 1–2 dm. high, the upper half or two-thirds floriferous; peduncle with several appressed, scarious, linear bracts 1–2 cm. long; pedicels single, subtended by scarious lanceolate bractlets 3 mm. long; pedicels 5 mm. long at anthesis, spreading, becoming 1 cm. long in fruit; involucre none; flowers perfect, hypogynous; perianth-segments distinct, white, petaloid, thinly membranous, obtuse, in two broadly overlapping series, 3 mm. long, the outer ovate, 1.2 mm. wide, 3-nerved, the inner elliptic, 1 mm. wide, 1-nerved; stamens 6, erect, distinct, inserted on the base of the perianth; filaments linear-oblong, flat, 1.5 mm. long; anthers 2-celled, linear-oblong, 1.1 mm. long; ovary slightly 3-lobed, conic, 2.5 mm. long, tapering regularly to the acute summit, 3-celled with about 8 ovules in each cell; styles 3, separate to the base, very short, with 3 capitate stigmas, the total length of both 0.4–0.5 mm.; capsule septicidal; seeds oblong.

Type, *Altson*, 326, collected from moist sandy crevices on boulders, in shade, Macreba Falls, Kurupung River, British Guiana, 28 Aug. 1925, and deposited in the herbarium of the Royal Botanic Gardens at Kew. *Altson* 393, collected a week later from the same place, exhibits mature capsules.

Smilax latipes n. sp. Stems climbing, the upper branches nearly free from prickles; petioles stout, twisted, 10–12 mm. long; stipules ovate-oblong, 5–6 mm. long, not usually cirriferous; leaf-blades firm, ovate-oblong, 12–18 cm. long, 4–8 cm. wide, acute, rounded at base, 3-nerved, with an obscure outer pair additional; veinlets prominently reticulate; flowering branches 15–30 cm. long, their leaves resembling the cauline but thinner and smaller; peduncles stout, flattened, 2–3 cm. long; umbels many-flowered; pedicels slender, 1 cm. long; segments of the staminate perianth spreading, oblong to oblong-elliptic, 4 mm. long, the outer series 1.5 mm., the inner 1.2 mm. wide; filaments flattened, 1.0 mm. long, 0.7 mm. wide at base, half as wide at the summit; anthers ovoid, acute, straight, 0.8 mm. long.

Type, *Gleason* 294 (staminate flowers only), collected at Tumatumari, British Guiana, 18 June–8 July, 1921, and deposited in the herbarium of the New York Botanical Garden. Two other specimens in the herbarium at Kew, *Schomburgk* 220 (159) and *Jenman* 4050, are also referred here. *S. latipes* is very similar in habit to *S. Schomburgkiana* Kunth, but differs in its much larger flowers and proportionately broader filaments.

Costus bracteatus n. sp. Stem stout, glabrous, height not stated, at least 1 cm. in diameter below; leaf-sheaths very finely scabrellate; ligules prolonged 6–10 mm. above the base of the petiole and 10–20 mm. on the opposite side, depending on the size of the leaf, finely veined, minutely pubescent, sparsely hirsute-ciliate; petiole differentiated, 4–10 mm. long, finely pubescent; leaf-blades oblanceolate, 33–39 cm. long, 9–9.5 cm. wide, the uppermost smaller, down to 14 by 4 cm., sharply acuminate, tapering from above the middle to the narrow but obtuse base, glabrous above, very minutely pubescent beneath or almost glabrous in the middle and upper parts; peduncles 24–30 cm. long, 11–12 mm. in diameter, strongly striate, conspicuously but finely pubescent; peduncular sheaths slightly shorter to slightly longer than the internodes, in one-third phyllotaxy, cylindric, not at all spreading, 4–5 cm. long on one side, 5–6 cm. long on the other, somewhat retuse at the summit on the shorter side, finely scabrellate to the touch, minutely pubescent under the lens, varying to nearly glabrous toward the base or perceptibly pubescent distally; spikes stoutly ovoid, 6–7 cm. long, 4 cm. in diameter, densely flowered, the rhachis half as long as the spike; bracts membranous, broadly ovate, appressed, 3–4 cm. long, essentially glabrous, their appendages recurved or spreading, ovate to elliptic, membranous, the lower 8 cm. long by 5 cm. wide, the upper reduced to ovate tips 1 cm. long and wide, veiny and minutely pubescent.

Type, *Jenman 6504*, collected on the Mazaruni River, March, 1892, and deposited in the Jenman Herbarium; a second collection is *Jenman 6818* in the same herbarium, collected in British Guiana without definite locality and labeled "perianth yellow, within finely veined in crimson." The species differs greatly from all others in the region in its long peduncle covered with leafless sheaths. The relation and grouping of the species depends on the location of the peduncle and this can not be determined positively from the specimens at hand. Apparently it is basal, since all species with terminal spikes, so far as known to me, are leafy to the spike, the upper portion of the stem is much smaller in diameter than the peduncle, and our plant bears a general habital similarity to *C. geothyrsus* K. Schum., in which the peduncle is definitely basal. If this interpretation is correct, *C. bracteatus* is the third known American species with this habit and differs from the Ecuadorian *C. geothyrsus* and the Peruvian *C. erythrocoryne* K. Schum. in the presence of terminal appendages on the membranous bracts.

Calathea fragilis n. sp. Herbaceous from a woody rhizome; leaves all basal, 2-6 in number; petioles incomplete, the upper portion flattened and grooved or deeply striate to the geniculus; geniculus smooth, almost terete, 7-9 cm. long; blades narrowly ovate, 61-63 cm. long, 29-31 cm. wide, rounded or subcordate at base but cuneate at the insertion of the petiole, convexly narrowed to an obtuse but apiculate apex, the apiculum 5-10 mm. long, glabrous; peduncles terete, glabrous below, becoming subtomentose distally, with one or two convolute basal sheaths as much as 2 dm. long and sometimes with a single, convolute, linear-elliptic, long-acuminate sheath 25 mm. wide and 20 cm. long about 15 cm. below the head; heads ovoid, appearing globose when pressed, 8.5-11 cm. long, densely flowered; bracts soft, membranous or subscarios, loosely appressed, unappendaged, finely longitudinally veined with numerous cross veinlets, the tissue very delicate or evanescent; outermost bracts broadly ovate, sessile and clasping, obtuse or subacute, 5-7 cm. long, 3-5 cm. wide, densely short-tomentose on the outside near the base, the remainder glabrous; upper bracts spirally imbricate, rotund, 4-4.5 cm. long and a little wider, the uppermost reduced to 2.5-3 cm. in length and width; bractlets erect, stiff, 22-26 mm. long, acuminate, with numerous longitudinal veins, fragile and fissile; peduncles 6 mm. long; bractlet (prophyllum) linear-subulate, triquetrous, slightly clavellate, 18 mm. long; sepals separate, connivent, lanceolate, 17 mm. long, 4 mm. wide, longitudinally veined, fragile; corolla-tube very slender, 18 mm. long; petals 3, elliptic, 15 mm. long, 5 mm. wide, acuminate, equal; exterior staminode broadly obovate-rotund, 12 mm. long, 9 mm. wide; cucullate staminode erect, oblong, 13 mm. long, with a recurved lateral acute process 2 mm. long; style stout, triquetrous, curved at the apex into a complete circle.

Type, *Altson 495*, collected at Erengtaru, Maicwac River, British Guiana, in forest on hill slope in red loam, alt. 1800 ft., April, 1926, and deposited in the herbarium of the New York Botanical Garden; name in Patamona dialect *Turura*; with the notes by the collector 'A tall herb. Leaves arising from a woody rhizome, 2-6 in a clump. Petioles 6 ft. long, blades 2 ft. long, 14 in. wide. Peduncle 20 in. long. Inflorescence ovoid, groups of (?) 5 flowers subtended by a chaffy bract. Flowers cream-colored. Fruit orange, trigonal, fleshy, 3-celled. Seed hard.'

Our plant clearly belongs in Petersen's section *Nudiscapae*, among the four other species with subulate bractlets, numbers 47-50 of Schumann's monograph. Of these, *C. altissima* (Poepp.

and Endl.) Koern. is most closely related, having also delicate fissile bracts, but differing in its narrower, sharply acute bracts more thinly pubescent, its shorter pubescent sepals, and larger corollas and staminodes.

Gymnosiphon breviflorum n. sp. Stems slender, simple, erect, 1-2 dm. high; leaves reduced to scattered elliptic scales 1 mm. long and 1-3 cm. apart; racemes geminate, separated by a terminal flower, 1-5 cm. long, 3-10-flowered; bracts elliptic, minute, obtuse; pedicels becoming 4-5 mm. long, or the uppermost a trifle shorter; perianth-tube slender, 4 mm. long, its three lobes ovate, 3 mm. long, soon dehiscent, the persistent base 6-nerved, becoming stoutly cylindric.

Type, *Hitchcock 17,349*, growing among leaves on the forest-floor, Tumatumari, British Guiana, 3-5 Jan. 1920, and conserved in the herbarium of the New York Botanical Garden; also *Barilett* without number from Kangaruma and *Jenman 7191*, in part, from the Mazaruni River.

Gymnosiphon guianense n. sp. Stems slender, simple, erect, 10-25 cm. high; leaves reduced to scattered elliptic scales 1 mm. long and 1-3 cm. apart; racemes geminate, separated by a terminal flower, 2-10 cm. long, 5-10-flowered; bracts minute, ovate, obtuse; pedicels rarely exceeding 2 mm. in length; perianth-tube 5-6 mm. long, tapering above, its three lobes ovate, 3 mm. long, soon deciduous, the tube truncate-conic, becoming 6 mm. long, conspicuously nerved above and subulate along the side of the ovary.

Type, *Im Thurn* without number, collected at Tukeit, Potaro River, British Guiana, 22 Feb. 1879, and deposited in the herbarium of the Royal Botanic Gardens at Kew. It is also represented by *Jenman 7191*, in part, *Lang 131*, and *Allson 304* from the Mazaruni River, *Abraham 216* from the upper Berbice River, *Barilett* without number from Onderneeming, *Appun 686* and *Jenman 1763* without definite locality.

All the species of *Gymnosiphon* hitherto known from north-eastern South America were described by Bentham in 1855 under the genus *Ptychomeria* and all the types may be seen in the herbarium at Kew. No species have been described since then and no attempt has been made at Kew to assign specific names to the Guiana material. Bentham's species differ markedly from the two described above in their smaller size, smaller and usually slender perianth, and reduced or capitate

inflorescence. Our two species, one of which appears to be widely distributed, may be distinguished at a glance by the combination of long pedicels and short flowers in *G. breviflorum* and short pedicels with long flowers in *G. guianense*.

Gymnosiphon *Altsoni* n. sp. Saprophytic; stem erect, simple, slender, from a single long slender root, 5-8 cm. high, beset at intervals of 6-8 mm. with lance-subulate appressed scales 2-3 mm. long; inflorescence a simple raceme of 1-3 flowers; bracts ascending, lanceolate, 3-4 mm. long; pedicels 1-2 mm. long; perianth-tube, including the ovary, 7-8 mm. long, 6-ribbed, slender, tapering toward the apex; perianth-lobes 3, ovate-lanceolate, spreading, 5 mm. long, white, yellow in the throat; filaments 0.6 mm. long, inserted in the throat; anthers 2-celled, 0.5 mm. long and wide, each theca somewhat constricted in the middle; style slender; stigmas 3, flattened, obcordate; corolla-limb circumscissile after anthesis just above the insertion of the filaments; ovary 1-celled with parietal placentae; ovules subglobose; capsule and seeds not seen.

Type, *Altson* 364, on the floor of the forest in sandy soil, Macreba Falls, Kurupung River, British Guiana, 30 Aug. 1925, deposited in the herbarium of the Royal Botanic Gardens at Kew. *Altson* 305, from the same locality, is identical. The collector notes that the stem is violet, the flower-buds brown-lilac, and the stigma violet. The species is included in *Gymnosiphon* with some reluctance. The plant has the aspect of *Campylosiphon* Benth., but its 1-celled ovary and wingless filaments place it in or near *Gymnosiphon* or *Dictyostega*. It resembles the former of these in the shape of the 3-lobed perianth and probably also in the seeds, provided that they maintain the same shape as the ovules. The known species of *Gymnosiphon*, however, have flowers in geminate clusters, and the corolla falls below the insertion of the filaments rather than above.

Some *Juncus* names

KENNETH K. MACKENZIE

I. CONCERNING *JUNCUS TENUIS*

Juncus tenuis Willd. (Sp. Pl. 2: 214. 1799), 'Habitat in America boreali,' is *Juncus dichotomus* Elliott (Bot. S. Carolina & Georgia 1: 406. 1817), and is not the plant appearing as *Juncus tenuis* in our current manuals. Dr. Diels, Director of the Botanical Garden and Museum at Berlin, has very kindly sent me from Willdenow's material portions showing the leaf-blade, the mouth of the sheath, the inflorescence, and the seeds. The leaf-blade is not flattened, and the auricles are rounded cartilaginous and not conspicuously prolonged.

I was brought to look into this matter by noting that Steudel (Syn. Pl. Glum. 2: 305. 1855) described *Juncus tenuis* Willd. as with 'vaginis adpressis ore nudis.' On the same page he described a new species *Juncus germanorum* ('*J. tenuis* Auctor. Germ.') as with 'vaginis laxiusculis ore in marginem membranaceum utrinque productis (ligulam mentientem).' This last, of course, is a very accurate description of the plant appearing in our manuals as *Juncus tenuis*.

Our current treatments of the *Juncus tenuis* group follow articles by Wiegand (Bull. Torrey Club 27: 511-527. 1900; 30: 446-448. 1903). From a systematic standpoint these articles are most admirable, and bring out the specific lines well, largely by the use of sheath characters. But unfortunately Wiegand made no attempt at all to look into the synonymy. Had he studied the work of Steudel he would not have made the statement that 'the characters used, it will be seen, are in many cases quite different from those commonly employed for the separation of species of *Juncus*.' In fact Elliott (*l.c.*) had used them as early as 1817, when he described what he took for *Juncus tenuis* as having 'stipules membranaceus, 1-2 lines long, bifid.'

Buchenau (Engler, Pflanzenreich 4⁸⁶: 115-120. 1906) followed Wiegand closely. His descriptions and illustrations are of a very high character indeed. In fact they are among the

best and most helpful in any group. Unfortunately he too does not seem to have always checked up the work of older authors.

Looking through the Index Kewensis and also through the synonymy given by Buchenau one finds a number of names given as synonyms of *Juncus tenuis* Willd. I have investigated the earlier of these names as follows:

(1) *Juncus bicornis* Michx. Fl. Bor.-Am. 1: 191. 1803. This species came from Georgia and Carolina. It is described as with 'foliis radicalibus, subsetaceis, canaliculato-planis' and 'involucro setaceo-2-phyllo erecto, paniculam terminalem parvulam superante.' It seems to me that Elliott (Bot. S. Car. & Ga. 1: 406. 1817), who more fully and very definitely described this species, did so correctly, and that the name *Juncus bicornis* Michx. is the name we should use for the species appearing in our manuals as *Juncus tenuis* Willd. Michaux referred to plates by Rostkovius (Monogr. Junc. 24. pl. 1. f. 3. 1801) and by Morison (Hist. Pl. 3: 228. Sect. 8. pl. 9. f. 15. 1699). Morison's early plate is based on a plant from Virginia 'Gramen junceum Virginianum calyculis paleaceis bicornis.' The illustration is not a good one, but it certainly shows flattened leaf-blades and I believe is quite properly referred here. It seems to me too that the plant illustrated by Rostkovius is also to be referred here or possibly to *Juncus Dudleyi* Wiegand.

The early illustration of *Gramen junceum elatius, pericarpis ovatis Americanum* by Plukenet (Alm. 179. pl. 92. f. 9. 1696) also belongs here, I believe. As far as I know this is the earliest plate of an American species of this group. An extraordinary thing is that Linnaeus cited both the above referred to plates of Morison and Plukenet in his original description of *Juncus nodosus* (Sp. Pl. ed. 2. 1: 466)—a species with which they have nothing in common. This was long ago noted by Rostkovius (*l.c.* 25).

A photograph of part of the original material of *Juncus bicornis* from 'Georgie' in Herb. Mus. Paris has been kindly sent me by Professor Lecompte. It bears Dr. Engelmann's identification '*Juncus tenuis* Willd. G. Engelmann 1869.' This particular specimen, however, does not answer the description of Michaux. The bracts are shorter than the inflorescence and the leaf-blades do not appear at all flattened. The auricles, too,

are apparently short and not prolonged. However, in view of the description in Michaux, it seems to me that we should use his name as did Elliott for the plant we have been calling *Juncus tenuis* Willd. Michaux had material from both Georgia and Carolina, and one is left with the impression that his description was not based on the Georgia material.

(2) *Juncus gracilis* J. E. Smith (Engl. Bot. 31. *pl.* 2174. 1810; not *J. gracilis* Roth Tent. Fl. Germ. 1: 155. 1788; not *J. gracilis* R. Br. Prodr. 259. 1810) seems to be the next name to be considered. This was based on specimens collected in Angusshire, Scotland. (The species occurs widely in Europe, where it is regarded as introduced.) The illustration of the leaf sheaths is of a conventional character, but as Smith (Eng. Fl. 2: 167. 1824) described the leaves as dilated and membranous at the base, I would regard this species as the same as *Juncus bicornis* Michx. as here treated.

Smith's name being a homonym, three other names were proposed by different botanists, each name being strictly synonymous with his. These names are *Juncus macer* S. F. Gray (Nat. Arr. Br. Pl. 2: 164. 1821); *Juncus Gesneri* J. E. Smith (Eng. Fl. 2: 167. 1824); and *Juncus Smithii* Kunth (Enum. Pl. 3: 349. 1841). The first of these is apparently the next name available for the '*Juncus tenuis* Willd.' of our floras, should *Juncus bicornis* Michx. turn out not to be available.

(3) *Juncus platycaulos* H.B.K. Nov. Gen. et Spec. Pl. 1: 190. (236 in smaller ed.) 1815. This was based on South American material collected 'in ripa Orinoci prope Atures et Caricharia.' According to Buchenau (Pflanzenreich 4³⁶: 117) this does not possess the 'auriculas magnas scariosas Junci tenuis' (*J. bicornis* Michx. as here treated), and apparently from a poor specimen it represents *Juncus dichotomus* Ell. It will be noted that its publication antedates that of *Juncus dichotomus* Ell.

II. CONCERNING JUNCUS SETACEUS ROSTK.

Juncus setaceus Rostk. (Mon. Junc. 13. 1801) is a species which has been most persistently misunderstood. It is based on an immature plant collected in Pennsylvania ('Habitat in Pennsylvania'), and is described as leafless ('J. culmo nudo'). It is said to be 'affinis valde praecedenti,' the immediately

preceding species being *Juncus filiformis* L. The number of stamens is not given. The perianth divisions are described 'petalis subulatis,' and 'apice subulato' and are figured with tips such as are very noticeable in young *Juncus effusus*, but not in young specimens of the plant we have been calling *Juncus setaceus*.

Rostkovius gives an illustration of his species (*pl. 1. f. 2*), which shows the upper part only of an immature plant.

It has been identified with a plant which has culms leafy at the base, and which is especially noticeable for its stiff, rigid, soon spreading perianth parts. This last mentioned plant is a coastal plain plant, reaching its northern limit in Delaware and the southern part of Cape May County, New Jersey.¹

While then neither the description given by Rostkovius nor his type locality fit the plant which has been passing under the name *Juncus setaceus*, yet description, type locality, and plate do fit the common Pennsylvania form of *Juncus effusus* L. Accordingly I am treating *Juncus setaceus* Rostk. as a synonym of *Juncus effusus* L. Engelmann (Trans. Acad. Sci. St. Louis 2: 444-5. 1866; Botanical Works 249) was much troubled about the identification of this species, but did not follow up the matter.

For the plant which appears in our manuals as *Juncus setaceus* Rostk. (Brit. & Brown, Ill. Fl. ed. 2. 1: 473. *f. 1184*; Small, Flora S.E. U. S. 258; Gray, Man. ed. 7. 272. *f. 575*; Buchenau in Engler, Pflanzenreich 4³⁶: 123) I propose the name ***Juncus coriaceus***, referring to the thick rigid texture of the sepals, petals and capsules. As a type may be designated a specimen in my herbarium collected by Henry Eggert, July 9, 1896, at Hot Springs, Arkansas, in swamps.

¹ In Tatnall's Catalogue of Plants of Newcastle County, Delaware (1860) p. 80, it is given as follows: 'Wet grounds; Appoquinimink. Rare.' In Cape May County, New Jersey it is 'of frequent occurrence, though local' (Stone, Plants of Southern New Jersey 332. 1911).

It is reported from Tinicum, Delaware county, Pennsylvania (Dr. George Smith) in Keller and Brown, Flora of Philadelphia (1915) p. 95, on the authority of B. H. Smith, and apparently this same record appears in Porter's Flora of Pennsylvania, p. 79. This material I am informed represents some species of the *Juncus tenuis* group.

III. CONCERNING *JUNCUS CANADENSIS* J. GAY

In *Rhodora* 6: 35-6. 1904 Professor M. L. Fernald well and carefully pointed out the distinctions between the stout plant with many-flowered heads, which he treated as *Juncus canadensis* J. Gay, and the more slender plant with few-flowered heads which he treated as *Juncus brevicaudatus* (Engelm.) Fernald. The former plant he stated is a plant 'commonest on the coastal plain from southern Newfoundland to Louisiana, and on the upper St. Lawrence and the Great Lakes, though it is occasionally found at other inland stations,' while the second plant 'abounds . . . from Newfoundland to the upper Saguenay, west to Minnesota, and south, mostly in cold bogs, to the mountains of Pennsylvania.' To this it may be added that the plant first referred to is found in acid soils, while the second is a strong calciphile.

Buchenau (Engler, *Pflanzenreich* 4³⁶: 160. 1906) objected to the application by Fernald of the name '*brevicaudatus*' to a plant with long-tailed seeds, and in its place took up the name '*J. coarctatus* (Engelm.) Buchenau.'

In looking this matter up, naturally the first question was to find out what *Juncus canadensis* J. Gay was, and whether the name should be applied to a very common and abundant Canadian plant, or to one local and uncommon there. The original description (in La Harpe, *Monogr. Junc. in Mem. Soc. Hist. Nat. Paris* 3: 134. 1827 [reprint p. 46]) calls for a plant

Spicis 4-8-16-floris . . . ; perigonii foliolis . . . capsula oblonga prismatica brevioribus. . . culmus 6-12 poll. altus . . . panicula composita, erecta, plus minusve coarctata vel laxiuscula . . . perigonii foliola lanceolato-linearia, substriata, acute aristata, interiora sublongiora. . . capsula ellipsoideo-prismatica, triquetra, utrinque leviter attenuata, vix mucronata.

It was divided into two varieties

- a. Culmo foliisque tenuibus, panicula sublaxa, spicis 10-15-floris remotiusculis.
- β. Culmo foliisque tenuibus, panicula coarctata, spicis 4-8-floris approximatis.

Specimens were cited 'Habite le Canada (herb. Michx.), la baie d'Hudson (Torrey), Terre-Neuve (La Pylaie).'

In our current manuals the name has been applied to a plant correctly described in Gray's *Manual* (ed. 7) as having

'stems stout 5-50-flowered heads sepals and petals awn-pointed, mostly shorter than the abruptly short-pointed capsule' (p. 274) and in the key (p. 269) 'capsule equaling or slightly exceeding the calyx.'

On the other hand *Juncus brevicaudatus* is there correctly described 'stem slender 3-7-flowered heads sepals acute, the petals rarely obtusish, much shorter than the prismatic gradually pointed deep-brown capsule' (*l.c.* 274) and in the key 'capsule much exceeding the calyx gradually tapering' (*l.c.* 269). It is very beautifully illustrated by Buchenau (*l.c.* 160).

Investigation of original material showed the following:

(1) A photograph of the Canadian material in Museum d'Histoire Naturelle at Paris collected by Michaux shows on one sheet one plant of *Juncus brevicaudatus* (Engelm.) Fernald and two small plants of another species. This sheet bears Dr. Engelmann's identification made in 1869 that the first mentioned specimen is '*Juncus canadensis* var. *coarctatus*' and the small plant is '*Juncus alpinus*, forma *pallida* depauperate.' The original label bears the wording 'Baye d'Hudson,' and shows that this locality attributed to Torrey by Gay really belongs to the immediately preceding citation from Michaux.

(2) Two photographs of the Newfoundland material of La Pylaie have been received. One from Museum d'Histoire Naturelle at Paris is of a sheet containing seven specimens. It bears the determination '*J. canadensis* var. *coarctatus* Engelm. 1869.' A sheet in the Kew herbarium contains two plants of La Pylaie material. These agree with the Paris material.

It will be seen from the above that all of the Canadian and Newfoundland material cited by Gay represents his variety β . They all represent the plant now generally called *Juncus brevicaudatus* (Engelm.) Fernald, as marked by Engelmann.

(3) The only material cited by Gay unaccounted for above is the Torrey material, incorrectly given as collected 'la baie d'Hudson.' Investigation at Paris did not result in finding any such material. A photograph from a specimen in the Hooker herbarium at Kew was received with the following note:

The right-hand specimens (the only ones photographed) are labeled *Juncus acuminatus* and that half of the herbarium sheet is endorsed in W. J.

Hooker's handwriting 'Dr. Torrey. *J. Canadensis* La Harpe.' They are probably not the actual specimens seen by La Harpe, but may possibly be duplicates of the same collecting.

As far as I can tell from the photograph, the specimens (four in number) are specimens of *Juncus acuminatus* Michx.

From the above it will be noted that no material seen by Gay has been found answering to our current interpretation of *Juncus canadensis* J. Gay.

The Canadian material collected by Michaux seems to me to be the type material of Gay's species, and accordingly I am proposing to use the name *Juncus canadensis* J. Gay in place of *Juncus brevicaudatus* (Engelm.) Fernald and *Juncus coarctatus* (Engelm.) Buchenau. In passing it may be noted that Gay's capsule description applies to this plant, and not to either *J. canadensis* of our manuals or to *J. acuminatus*. It reads, as quoted above, 'capsula ellipsoideo-prismatica, triquetra, utrinque leviter attenuata, vix mucronata.'

The only evidence found tends to the belief that *Juncus canadensis* var. *a.* J. Gay was based on specimens of *Juncus acuminatus* Michx., but in view of the non-conclusive character of this evidence this conclusion must be regarded as tentative only.

For the plant which has been appearing in our manuals as *Juncus canadensis* J. Gay I am proposing to use the appropriate name ***Juncus longicaudatus*** (Engelm.) n. comb. (*Juncus canadensis* var. *longicaudatus* Engelm. Trans. St. Louis Acad. Sci. 2: 436. 1866 and 2: 474. 1868).

I am under obligations to Prof. H. Lecomte of the Museum d'Histoire Naturelle at Paris and to Dr. Arthur W. Hill, director of the Kew Gardens, for photographs of the material here referred to.

IV. WHAT IS *JUNCUS BREVICAUDATUS* (ENGELM.) FERNALD?

Juncus brevicaudatus (Engelm.) Fernald goes back to the following few words

J. Canadensis Gay

a. brevicaudatus (*J. acuminatus* Gray)

A. coarctatus. Pennsylvania, northward and north-westward.

B. patulus. Pennsylvania to western New York and Ohio.

(Trans. Acad. Sci. St. Louis 2: 436. 1866; Engelmann's Botanical Works 245.)

The name was quickly abandoned by Engelm. (Trans. Acad. Sci. St. Louis 2: 474. 1868; Engelm. Bot. Works 263) as Buchenau (Pflanzenreich 4³⁶: 160) points out.

However, Buchenau is in error in stating that the name was *nomen nudum*, because Engelm. did cite Gray's '*Juncus acuminatus* Michx.' This reference is to Gray's Manual ed. 2. 481. 1856). There the description given is, I believe, mostly if not entirely of what we have been calling *Juncus brevicaudatus*. Under the circumstances the name *J. brevicaudatus* (Engelm.) Fernald, although most inappropriate for a plant with long-tailed seeds, can logically be used as in our current manuals. The other way is to proceed on the belief that Engelm. must have based the name upon some specimen of his *J. Canadensis* a *brevicaudatus* B *patulus* which later became his *J. canadensis* var. β *brachycephalus*. (Trans. Acad. Sci. St. Louis 2: 474. 1868; Engelm. Bot. Works 263-4). This is a plant with short-tailed seeds, and one to which Engelm.'s first name is very well applicable. Gray's description too of his *Juncus acuminatus* Michx. calls for a plant with 'abruptly acute pod,' leading one to believe that he included *Juncus brachycephalus* (Engelm.) Buchenau in his conception of Michaux's species. If this last course is pursued the name becomes a synonym of *Juncus brachycephalus* (Engelm.) Buchenau Monogr. Junc. 268. 1890. I am inclined to believe that this would be the best course.

The name taken up by Buchenau, *Juncus coarctatus* (Engelm.) Buchenau (*l.c.* 160), goes directly back to *J. canadensis* β J. Gay, and is strictly synonymous with *J. canadensis* J. Gay, as I interpret it.

The use of osmic-impregnation methods in plant cytology

ROBERT H. BOWEN

(WITH PLATE I)

The use of osmic acid for the purpose of blackening certain kinds of cytoplasmic elements has been a familiar method in animal cytology for many years. This is particularly true of the blackening of certain types of fat-materials, which often occurs upon the addition of osmic acid or mixtures containing it. But a much more important effect, and one concerning the chemistry of which very little is known, is the blackening of various lipoidal structures after prolonged exposure to aqueous solutions of osmic acid. This effect was observed certainly as long ago as 1888 by Prenant, but the real significance of the method was first made known by Kopsch ('02). This worker discovered that by immersing animal tissue in 2 per cent osmic acid for periods of several days (or weeks) it was possible to blacken the so-called Golgi apparatus in a most selective manner. This reaction was further studied by Sjövall ('06), who sought to improve the very poor fixation effected by the action of osmic acid alone, by first fixing the material in formalin and subsequently subjecting it to the osmic treatment. This separation of fixation from the osmication step was further studied by Weigl ('10) and finally perfected by Kolatchev ('16). By these methods, now familiar to all animal cytologists, it is possible to effect a blackening of the Golgi material in all kinds of animal cells. This blackening in animal cells is usually restricted to Golgi material, but under certain conditions, which are not yet very well understood, the mitochondria may be blackened, and occasionally other structures. In fact, by a slight variation in one of the usual methods Hirschler ('25) obtained a sharp blackening of the nuclear membrane. It is to be distinctly understood, however, that such results in animal cells are the exception—the rule is that the Golgi apparatus alone is almost invariably the only structure to show a distinct blackening.¹

¹ This statement does not apply to Protozoa, which present technical problems all their own.

Some of these osmic methods have now been shown to yield results of truly remarkable excellence, when properly handled. Considering the interest which attaches to certain problems connected with the Golgi apparatus, it is remarkable that for over twenty years after its identification in animal cells, practically no effort was made to examine plant material for its occurrence. This is even more difficult to understand, in view of the extensive and controversial literature which had been accumulating on the side of animal tissues. The obvious thing to undertake was clearly the effect on plant cells of these same osmic methods. This was first seriously tried by Nassonov ('18), who applied the method worked out by Kolatchev to various kinds of plant cells. He observed that the plastid-forming bodies in meristem cells were frequently selectively blackened, and that at other times cytoplasmic networks especially associated with the division figures were demonstrated.

Somewhat later (Bowen, '26), I repeated Nassonov's work, using other methods as well as the one employed by him, and found to my astonishment that in different cells it was possible to obtain a precise blackening of practically any cellular structure with the exception of chromosomes in mitosis. Much the same result was reported almost simultaneously by Guilliermond ('26). There is thus placed in the hands of cytologists a method of technical attack of the greatest interest and value, which permits the study of certain cytoplasmic structures otherwise undemonstrable, as well as providing further means for the study of structures already well known.

In view of the fact that most of the work on plant cells by these methods has been done thus far in zoological laboratories, it has seemed to me that botanical workers might welcome some report of the methods arranged particularly for their own purposes. For this reason the present paper has been prepared. In it I shall give detailed directions for the methods which have been shown to work successfully, together with some analysis of the results obtainable. More detailed reports on specific cytoplasmic structures may be found in two of my recent papers (Bowen '28, '29). The methods of osmic impregnation which have proved useful are primarily those of Kolatchev ('16) and of Weigl ('10). Hirschler ('24) has published a variation of the

Kolatchev method with which I have experimented only a little. In general it yields results much like those of the Kolatchev technique.

GENERAL NOTES

The methods of osmic impregnation require rather more careful manipulation than is called for by most of the orthodox cytological techniques, and certain things are so indispensable that special attention will be called to them in the beginning. I should add, however, that the laborious methods of dehydrating and embedding still common in the botanical laboratory are only a waste of time with osmic technique. Reasonably careful handling such as is adequate for routine work in animal cytology is all that is necessary. The osmic methods are so tedious, so variable, and so often unsuccessful, that it is useless to introduce technical refinements at the present stage of their development.

1. Material for osmic work should be absolutely fresh. Do not use plants which have lingered about the laboratory or greenhouse under unfavorable conditions. Use pieces of material as small as possible. Large root-tips and other massive parts will probably not react successfully unless subdivided.

2. Use osmic solutions, both for fixing fluids and for the osmication process, which are positively fresh—not over one to two weeks old—and which have been kept properly clean and preserved from the action of light.

3. Keep the ingredients of fixing fluids in separate stock solutions, and mix them only just before using.

4. All fixation, and especially all osmication steps, *must positively be conducted in glass-stoppered bottles*. If these are not available do not waste time trying these methods. They will not work with cork-stoppered bottles. The glass-stoppered bottles should not be so large that extensive air-spaces are left above the fixing reagents. The most convenient size for plant work is a bottle containing (when completely filled and the stopper in place) about 4 cc., with a mouth sufficiently wide to permit the easy introduction of a pipette. Such bottles are carried in this country by Eimer and Amend of New York City, from whom I have regularly obtained them. After using a bottle for any purpose, wash it in cleaning fluid, and rinse

it under the tap with scrupulous care, finally rinsing in distilled water before drying. Carry on fixation and osmication in the dark. This is most easily done by keeping the bottles in cardboard boxes with deep covers.

5. Once the material has been put in the fixative, handle it thereafter only with wide-mouth pipettes. The use of forceps is very bad after osmication because the tissue becomes brittle and is easily damaged.

6. After the material is finally washed out in running water after osmication, do not spend more than five or six days at the most in the alcohols before embedding in paraffin. For these steps immediately prior to embedding, it is convenient to carry the material in small shell-vials with cork stoppers. After osmication, this use of cork stoppers does no harm.

THE KOLATCHEV METHOD

The essentials of this method were published in 1916 by Kolatchev. The routine here described follows the procedure used by Nassonov ('18) on plant material, with certain variations that I have found useful.

1. Fix for 24 hours in Champy, as follows:

1 per cent chromic acid	7 cc.
3 per cent potassium bichromate	7 cc.
2 per cent osmic acid	4 cc.

Do not overload the fixing bottles. About 10-15 root-tips not larger than those of *Hyacinthus* can be safely placed in 3 cc. of fixative. The bottles should be occasionally agitated gently to assist in the penetration of the fixative.

2. Transfer to a dish of tap water to remove the excess of fixing fluid, and then wash in running water for 24 hours. This step is important, and the washing out of the chromium compounds must be complete. A convenient method for performing this step with large batches of material has been elsewhere described (Bowen, '27a).

3. Transfer the washed material to a dish of distilled water, and thence to fresh glass-stoppered bottles for osmication. In order to avoid dilution of the osmic acid, I find it convenient first to transfer the material to an empty bottle, draw off all the distilled water which may have been carried over, with a

pipette, and then add the osmic acid. About the same relations should obtain between material and volume of osmic acid as in the case of fixation. Do not be stingy with the osmic solution, it is poor economy. The osmication step may be carried out in several ways. I usually separate the material while in distilled water and proceed to try four variations of osmication, as follows.

- I. Place the material in 1% osmic acid solution, and then:
 - a. Put the bottles in an incubator at 35°C. for periods of 4 to 9 days.
 - b. Put the bottles in an incubator at 40°C. for 8 hours, and then transfer the bottles to an incubator at 35°C. without any change of the osmic solution. Leave in this second incubator for periods such that the total time in osmic acid is from 4 to 9 days, as before.
- II. Place the material in 2% osmic acid solution, and then proceed:
 - a. As in method Ia.
 - b. As in method Ib.

I usually carry along all four variations simultaneously. If for one reason or another this is not feasible, probably the best single variation is IIb. In general this offers the best probability of a successful impregnation, but material varies in its behavior and I have found it up to the present time useful to try all the possibilities. After a longer or shorter period in the incubators, the osmic solution almost invariably begins to blacken. This is of no consequence until it becomes very pronounced, and then it is best to pour off the blackened solution, rinse out with distilled water and add fresh osmic solution; or better, rinse the material in distilled water and transfer to a clean bottle with fresh osmic acid. The temperatures of the incubators need not be absolutely exact, but a range of more than one degree above or below the temperature advised, should be avoided. It is well to take the bottles out of the incubator daily and agitate each one gently to assist in the penetration of the osmic solution.

4. When the preceding osmication step is completed, the material is transferred to running water for 24 hours. This washing is less important than that in step 2, but it is well to see that the osmic solution is removed before proceeding.

The time at which to terminate the osmication is the one difficult variable in this method. There is no way to tell when a successful impregnation of anything whatever has been attained. This is a serious difficulty, because if the osmication period is too short, nothing will be blackened, and if too long, a serious over-blackening occurs which usually ruins the material for critical purposes. One is therefore driven by necessity to a method of trial and error, which is very laborious but which alone can give one any satisfactory idea of the success of his procedure. I proceed as follows. Each day, beginning on about the fourth day of osmication, two or three samples are removed from each bottle, with a wide-mouthed pipette.² This is repeated daily up to the eighth or ninth day of incubation, by which time the contents of the bottles will be exhausted. The samples thus obtained are washed and carried along separately. After embedding, section samples near the beginning and end of the osmication period, and at some intermediate point. With a little experience, an inspection of the sections will indicate at once where the best result, if any, has been obtained and one can govern further sectioning operations accordingly. As one becomes acquainted with a particular material, the most probable times for a good impregnation become more definite, but a certain amount of trial by sampling is always advisable, for slight differences in the results of osmication are the rule rather than the exception.

5. The material having been washed as noted in the preceding step, it is then run up and embedded in paraffin. Unlike silver impregnation, osmic blackening is very stable, and no unusual precautions are necessary:

6. Cut sections not over 5 micra thick.

7. When the slides are ready, remove the paraffin in xylol, pass down to absolute alcohol, to insure complete dehydration, and then back to xylol and mount in balsam as usual. For routine work this direct method of mounting is generally sufficient. One may, however, wish to bleach or to counterstain the sections, in which case proceed as described on pages 41 and 42.

² Be very careful to use a pipette which can not in any way be contaminated with a chromium compound. It is best to reserve a particular pipette for this step.

THE HIRSCHLER METHOD

This method, although worked out independently by Hirschler ('24), is essentially a variation of Kolatchev's procedure. The steps are practically the same as in the Kolatchev method, with the exception of the osmication stage. It is Hirschler's belief that a prolonged osmication at a lower temperature is better than the rapid osmication as practiced by Kolatchev. Hirschler accordingly osmicates (step 3, page 36) in 2% osmic acid at 20° to 25°C. I have used room temperature, also an incubator at 25°C. Osmication progresses very slowly, and samples may be removed over a long space of time. I have followed the course of events (at 25°C.) at intervals of every other day from the fourth to the thirty-third day of osmication. No results of any particular use were obtained before the sixteenth day, and longer osmication periods are more successful.

THE WEIGL METHOD³

The basis of this method was worked out by Weigl in 1910, but the details of its manipulation were never published by its inventor. A number of later workers have experimented with its possibilities, and the following directions represent the variation which I have used on plant material.

1. Fix in corrosive-osmic, the usual proportions being as follows:

1 per cent osmic acid	1 part
Mercuric chloride, saturated solution in 0.75 per cent aqueous sodium chloride	1 part

With some kinds of plant material this fixative blackens within fifteen minutes. In case this occurs, pour off the blackened fluid and add fresh fixative, repeating if necessary at a later time. The length of fixation is an important variable in this method, but it can be arrived at only by trial. I usually fix material for periods of 1, 2 and 4 hours. Shorter or longer periods might be tried, but the ones named are most likely to fall within the period of possibly good fixation. It is also

³ This method is frequently called by animal cytologists, the Mann-Kopsch method. Since Weigl alone is responsible for the essential steps, it has seemed to me shorter and better to name it after the inventor—the Weigl method.

possible to vary the proportions of osmic acid and mercuric chloride in the fixative, but results on animal tissue do not seem to indicate that much is to be expected from such experiments.

2. After fixation (the batches of material from each fixation period being of course kept separate), wash in running water for 30 minutes. Longer washing will do no harm but is not necessary.

3. Then transfer the material to distilled water and thence to the osmic solution. Osmicate in 2% osmic acid. This may be done at room temperature, but in order to eliminate controllable variables as much as possible, it is best to use an incubator at 25°C. As in the Kolatchev method, the osmication step is subject to wide variations, and the best procedure is to remove samples daily from the third to the eighth day. Handle this part of the technique exactly as described under the Kolatchev method (p. 38).

4. Samples removed from the osmic solution are washed for 24 hours in running water.

5. Then pass up through the alcohols, embed, section and mount, as described under the Kolatchev method (p. 38).

6. If it is desired to bleach or counterstain, see pages 41 and 42.

General result. Sections from material prepared by any of the osmic methods have a characteristic appearance. The structures which may have been successfully impregnated are usually an intense black, but sometimes are only grayish. The remainder of the preparation usually assumes a characteristic yellowish tone, although in exceptional cases the background may be almost colorless. The nucleus is easily distinguished, and chromosomes in division stages can usually be recognized without difficulty. Cell walls may be very sharply delimited, but this is not always the case. Faulty impregnations may show a good deal of granular blackening of the cytoplasm, and from this point the results may grade on down to the impossibly poor. A great deal of experience is necessary in order to judge the probable degree of success of a particular preparation, and no rules can be given. The skillful technician and competent observer will gradually learn the ear-marks of a successful osmic preparation, and until some proficiency in

this matter is attained it is easy to commit serious errors of identification and interpretation.

BLEACHING METHODS

Although the direct mounting of sections from osmicated material is the general rule, it is sometimes useful to clear up the background by bleaching. This process often results in preparations of amazing brilliance, but it is perhaps questionable as to how much the picture is improved for purposes of critical study. Certainly, bleaching will not make first-class preparations out of slides which are not pretty good to begin with. Nevertheless, bleaching is worth trying on occasion and for some methods of counterstaining may be essential. There are three bleaching processes in common use:

The turpentine method. Remove paraffin from the sections in xylol and transfer the slides to double rectified oil of turpentine. Bleaching occurs very slowly. Examine the slides occasionally under the microscope and when the proper point is reached wash the slides thoroughly in xylol and proceed as usual to mounting. The time required by this method will be anywhere from 12 to 48 hours. The action of the turpentine must be checked before it has appreciably attacked the blackening of the particular element one wishes to study.

The hydrogen peroxide method. Run the sections down to water, and bleach in a solution of hydrogen peroxide made by adding 2 drops of the common medicinal solution to 50cc. of distilled water. The action is very rapid and must be controlled with the greatest care. Usually the time required is from 15 to 60 seconds, and even with such short exposure to peroxide, the blackening of the desired elements may be seriously affected. Check the bleaching action by a thorough washing in running water (10 or 15 minutes), and then run up and mount as usual.

The permanganate-oxalic acid method. A variation of this old bleaching process is perhaps the best method at present available. I have used it extensively on plant material and find it a most desirable technique, although a little more complicated than the preceding methods. I should recommend it as the method of choice for bleaching.

1. Run sections down to water.

2. Bleach in 0.1% aqueous potassium permanganate. The sections acquire a brownish tone and the osmic blackening is rapidly attacked. The extraction must be very carefully controlled under the microscope. Usually about 10 to 60 seconds is sufficient time. In some cases, visual examination is very difficult and it is often an advantage to experiment with one's watch as the controlling element. Once the proper time is determined, the remaining slides can be very quickly handled without individual inspection.

3. When the proper point in bleaching is reached, wash *quickly* in distilled water and place at once in 0.1% oxalic acid solution. Here the slides should remain until the brown color acquired in the permanganate has disappeared—about one or two minutes.

4. Then wash at once in running water for ten or fifteen minutes, run up and mount as usual.

The results are very fine, and with a little experience few serious mistakes in differentiation will be made. The permanganate solution goes bad very quickly after using, and fresh solutions should be used each time a batch of slides is to be treated.

COUNTERSTAINING

The value of counterstaining osmic preparations of plant material is something of a question because of the limited work which has thus far been done with these methods. Clearly, counterstaining is usually of little value in routine work and as it almost always involves a great deal of time, it seems scarcely advisable to have recourse to it unless with a definite purpose in mind. As a matter of fact, osmicated tissues are very refractory toward stains of every kind and counterstaining is always difficult. Preparations which are not first-class to begin with, are useless for counterstaining, and it is time wasted to try them. Sometimes fairly good results are obtainable by direct staining of osmicated material, but more often it is better or even necessary to bleach first. If the impregnation is faint, bleaching must perforce be omitted anyhow, but such weak osmications are usually accompanied by a better staining capacity of the material, and bleaching is, therefore, less necessary. One finds, as a matter of fact, that the heavier the osmic

impregnation, the less affinity do the sections have for stains. Conversely, the more complete the bleaching, the better the staining result. Unfortunately just as the tissues begin to take the stain in a really satisfactory manner, the impregnation shows an appreciable extraction, and the bleaching must needs be checked before the tissue is in condition for a first-class stain. The use of a counterstain is thus a matter requiring experienced judgment and this can only be acquired by many trials and errors.

For a general contrast stain, anilin dyes such as eosin, light green or orange G, made up in 95% alcoholic solution may be used. These may give a pleasing color-contrast, but do not add materially to the value of the preparations for critical study. The most valuable stain, indeed the only one of any real worth, is acid fuchsin. This may be employed according to any of the Altmann modifications, but as Nassonov ('18) showed, variations of the Kull procedure are the best. By this method it is possible to stain nuclei and chromosomes, and also the chondriosome-like bodies in the cytoplasm. Of these latter elements, those which are capable of producing plastids are less readily stained than the other type—often called chondriosomes by botanical cytologists. Two ways of applying the Kull method may be used, as follows:

1. Run the sections down to water and bleach or not, as one chooses, by the permanganate-oxalic acid method.
2. Stain in Altmann's acid fuchsin. I flood the slide with stain, and then warm it carefully over a flame until vapors are given off. Cool the slide for 2 or 3 minutes, and repeat the warming process.
3. After a total time of about 5 minutes in the acid fuchsin, wash off the stain completely in distilled water.
4. Differentiate in a 0.5% solution of aurantia in 70% alcohol. The time required is usually less than 1 minute, but no rule can be laid down, and the only safe procedure is to examine the slide under the microscope and check the differentiation at the desired point. When one is doing routine staining on a large batch of similar material, it is often easier to differentiate by the clock, having first obtained the approximate time by trials.
5. When the slide is differentiated to the proper point, rinse

it very quickly in 95% alcohol, then 100% alcohol and transfer finally to xylol. Mount as usual in balsam. The 95% alcohol may be omitted. In any event the dehydration must be effected in the shortest possible time—a few seconds at most.

The preceding method stains the nucleus and chromosomes red, and on some occasions will stain cytoplasmic elements also, provided these have not been blackened by the osmic acid. In general, however, cytoplasmic elements which have not been impregnated can only be stained by the complete Kull technique. This raises a difficulty, since in osmicated material the thionin (or toluidin blue) takes so heavily that a properly balanced differentiation can usually not be obtained. In general therefore, to use the second staining procedure, one must have recourse to bleaching, the usual method for this purpose being the permanganate-oxalic acid technique. The second method for using Kull is, therefore, as follows:

1. After bleaching and thorough washing (5 or 10 minutes) in running water, stain in Altmann's acid fuchsin exactly as in the first method.

2. Rinse off completely in distilled water and flood the slide with a 0.05% aqueous solution of thionin. Stain for about one minute. Sometimes a much shorter time is required, but this must be ascertained by trial and no definite rule of any kind can be given. If the staining time is too long, it will be impossible to remove the blue color sufficiently from the cytoplasmic background before the fuchsin stain is too much extracted.

3. Rinse off again in distilled water, and differentiate in aurantia as in the first method. This will usually require less than 30 seconds. In my own work, I have frequently found 10 seconds a sufficient time.

4. Dehydrate quickly, as in the first method, and mount as usual in balsam.

Unfortunately, acid fuchsin preparations of this type are not very permanent, the stain being lost sometimes in a few months. More favorable examples may last a year or two.

In view of the fact that the more complete the bleaching, the better the stain obtainable with acid fuchsin, it may be possible to salvage preparations in which the impregnation has failed, by completely bleaching and then staining by the usual Kull method. If one's material is limited and preparations of

the chondriosome-like bodies in the cytoplasm are very much desired, this method may be of assistance. In general, however, I think it is not to be recommended as a first-class working procedure.

GENERAL RESULTS

It is in general impossible to predict exactly what will be blackened by these osmic methods in any particular case. Sometimes one type of result is obtained, and in another trial of the same material the result may be different. Or, more probably, in one and the same section—even in adjacent cells—the elements impregnated will be different. This may be very discouraging to some workers who still cling to a faith in specific staining methods, but to one whose interest is in the result rather than the method, osmic impregnations are of extraordinary interest. In some kinds of material it is possible on occasion to get an impregnation of practically all the known structures in the cell. Thus one is enabled to study now one element, now another, in different cells of the same preparation; or one may get various combinations of different elements simultaneously demonstrated in the same cell. One thing only is absolutely essential in the study of osmic impregnations, and that is a trained judgement gained by experience. By repeated trials, by extended study of one's material, and by comparison with preparations made by the more customary methods, it is possible to effect a complete separation and identification of all the blackened elements. With this general caution as to the nature of osmic impregnation in plant cells, some more specific statement of the results may be attempted.

1. These osmic methods were originally designed for the demonstration only of the animal Golgi apparatus, and, as noted in the beginning, they are quite remarkably specific in animal cells. We might, therefore, expect a similar action in plant cells, at least to the extent of demonstrating one element in plant cytoplasm with unusual regularity. Such is actually the result obtained. These methods most frequently and regularly blacken a collection of cytoplasmic bodies to which I have tentatively applied the name of 'osmiophilic platelets.' These are probably a new category of cytoplasmic elements, hitherto unnoticed by botanists because they can,

as a rule, be demonstrated only by osmic impregnation. These have been fully described in another place (Bowen '28), where details as to their structure, etc., may be found. The most common result of osmic impregnation is, therefore, the demonstration of the osmiophilic platelets alone. This has now been effected in bryophytes (fig. 1, and also Bowen '27b), pteridophytes (Bowen '28), gymnosperms (unpublished), and angiosperms (fig. 2, and also Bowen '28). The best results are obtained by the Kolatchev (or Hirschler) method, the Weigl method yielding picutres which are usually distinctly inferior.

2. In some kinds of material, the root-tips of *Equisetum* for example, almost no results are ever obtained except on the osmiophilic platelets. But in other cases, due apparently to a differing cytoplasmic setting, other elements are blackened, sometimes with marked regularity. Of these perhaps the one most commonly impregnated is the plastidome. This term is taken to include the primordial bodies (pro-plastids or archiplasts) in meristem cells from which plastids will later develop, and also fully differentiated plastids of various kinds. The plastidome may be blackened alone (fig. 6), as noted also particularly by Nassonov ('18), but in my preparations of meristem cells the osmiophilic platelets were very frequently demonstrated simultaneously (fig. 3). The Kolatchev method is again the most favorable, but similar results are sometimes obtained by the Weigl method (fig. 5).

3. A very common result, in some kinds of cells it might be said to be a uniform result, the vacuoles (vacuome) may be very clearly demonstrated. This may be effected by an intense blackening of the whole vacuome (figs. 8 and 9), or there may be only an indefinite grayish network marking out the vacuoles (lower part of fig. 4). Sometimes the vacuoles are brought out merely as clear spaces by contrast with a darkened background (upper part of fig. 4). Blackening of the vacuome seems to depend largely upon its contents. In bryophytes, and in pteridophyte root-tips results are very rare, while on certain angiosperm roots constant success is the rule. The method also plays a rôle, and in the case of the vacuome I found the Weigl method most useful. Thus on *Ricinus* root-tips the Weigl method regularly gives results, while the Kolatchev method is relatively useless. In case the vacuome is impregnated, a

simultaneous blackening of the osmiophilic platelets is apt also to occur (fig. 8).

4. Perhaps the most uncommon result is the blackening of those cytoplasmic elements which botanical cytologists frequently call chondriosomes, or 'inactive' chondriome, but which I have temporarily referred to as the pseudochondriome (Bowen '29). These bodies are almost always of a spherical form in meristem cells. Practically the only place where I have found them regularly blackened (by the Kolatchev method) is in the outer plerome of the hyacinth root-tip (fig. 7, which shows also the delicate, thread-like archiplasts). However, they may appear sporadically in other places, for instance the plerome of *Hordeum*, and they are quite regularly blackened in the very old cells of the root-cap of angiosperms at the very apex of the root-tip. In this location, however, the impregnation is not of much use for purposes of study.

5. In addition to these definite cytoplasmic components, cytoplasmic impregnations of a quite different type are commonly found, especially in late prophase and the metaphase of mitosis in meristem cells of angiosperm root-tips. This result was first noticed and fully described by Nasonov ('18). It consists of a very definite blackening of what appears in resting cells to be a cytoplasmic network. In dividing cells the polar caps are also demonstrated as well as the fibers which are attached to the chromosomes (fig. 10). This latter result is most astonishing, and, as Nasonov showed, the number of chromosomes can actually be determined by counting the number of blackened fibers as seen in cross-sections. The whole history of the division figure can be followed, and an exhaustive study of osmic preparations would doubtless yield most interesting results on the nature of the polar caps and other oft-debated features of mitosis in higher plants. When this particular type of blackening occurs, other cytoplasmic elements usually are not demonstrated, but sometimes the plastidome, and in *Hyacinthus* the pseudochondriome, may be in part blackened.

Occasionally, in telophases, the cell-plate may be impregnated, and this may be the only thing blackened in the whole cell (figs. 12, 13). Sometimes the osmiophilic platelets are simultaneously, though inadequately, demonstrated.

6. Impregnation of the nucleus and nuclear structures is a

less common result, but occasionally occurs in a sporadic way in angiosperm root-tips. The whole nucleus may be solidly blackened, with the exception of the nucleolus (lower cell in fig. 11). The nucleolus seems never to be blackened as a whole, but not infrequently one or more granules within the nucleolus are blackened (fig. 11). The exact results vary somewhat but need not here be mentioned in detail, since their meaning is quite unknown. Sometimes a selective blackening of the nuclear membrane is obtained, the remainder of the nucleus being quite unaffected.

7. A very common result especially in cells of the root-cap and central plerome, is the very selective and intense blackening of bodies located within the vacuoles. These are clearly the coagulated masses so often described by Dangeard and Guilliermond. One of the best ways to demonstrate them is by the Hirschler method with brief osmication (4 to 8 days); or better still by fixing according to the Weigl method for 24 hours, and then omitting the osmication step entirely.

8. The osmication methods are known in animal cells frequently to give no result on fatty material. In the case of plant cells, likewise, satisfactory results on the so-called lipoidal granules have not yet been certainly obtained.

9. Here it should be again noted that all sorts of combination results may occur. In these cases, the osmiophilic platelets usually are demonstrated, but not invariably. Thus we may get platelets and plastidome; platelets and pseudochondriome; platelets and vacuome; pseudochondriome and plastidome; platelets, plastidome and pseudochondriome; vacuome and plastidome; vacuome, platelets and plastidome; and still other combinations with the nuclear structures, etc. With some previous knowledge of the cytoplasmic situation in plant cells, however, the analyzing of most of the ordinary impregnation results will present no serious difficulties to the experienced observer.

10. Finally, in the case of counterstaining with acid fuchsin, the resting nucleus and the chromosomes in dividing cells will be regularly stained in red. Preparations in which either the pseudochondriome or the plastidome, or both, have failed to blacken, may, upon proper counterstaining, present these unblackened elements in red.

OTHER NOTES

The results of work with these methods by others are in the main of a similar nature. Nassonov ('18) with the Kolatchev method reported the impregnation of the plastidome alone, and also the blackening of the cytoplasmic network and of the division figure in mitosis. Gatenby ('28) in a recent note corroborates my findings with the Kolatchev method on the osmiophilic platelets. He reports that in addition to the usual Champy fixation in step 1, the following slightly modified fixative also gives very good results:

1 per cent chromic acid	} equal parts
6 per cent potassium bichromate	
2 per cent osmic acid	

The only other worker to report on the osmic methods as applied to plant tissues is Guilliermond ('26, '27). His results include many kinds of cellular components, and so are of particular interest for purposes of comparison with the bulk of this paper, which represents my personal experience. In one important respect his technique differs from that of Gatenby, Nassonov, and myself, and his findings are also different in certain important respects. He used particularly the method of Kolatchev, with one very important change in procedure. He osmicates in 2% osmic acid for 8 to 15 days (or more) at 40°C. Such treatment would ruin any animal tissue I have ever experimented with. As it is, Guilliermond finds that the sections are completely blackened and he then endeavors to differentiate for the cytoplasmic features, particularly the vacuome, by bleaching according to the permanganate-oxalic technique. This method of handling osmic acid is not recommended by any of my own experience, and it may be the reason for some of Guilliermond's anomalous results. Thus he does not mention the osmiophilic platelets, and finds, further, that the pseudochondriosomes are easily and regularly blackened together with the plastidome. His figures of such simultaneous impregnations are certainly not like the appearance of my own preparations. He states that the method rarely blackens the vacuome in higher plants, and then only after an osmication of 15 days. He finds that aleurone grains are beautifully impregnated, and also the vacuome in some of the thallophytes. It is

evident, therefore, that so far as the general possibilities of osmic impregnation of plant tissue are concerned, Guilliermond's results substantiate what I have said about their usefulness. In certain details his results are markedly different from my own and those of Gatenby, but on the other hand his very unusual handling of the osmication step may have been the cause of these differences.

SUGGESTIONS FOR PRACTICE

Osmic impregnation is so erratic in many of its characteristic effects, that one unacquainted with its use would certainly do well to begin with some material where the conditions are known and where a successful result of some kind is reasonably to be anticipated. The best material I know of is the lateral root-tips of *Vicia Faba*, from seeds germinated both in earth and in a moist chamber (Nassonov ('18), Bowen ('28, '29)). Use only the tips of roots not over an inch in length. If the technique is properly carried out, the osmiophilic platelets are almost certain to be demonstrated, together with a variety of other results probably depending on unknown conditions of many kinds. It is my own belief at present that the osmiophilic platelets are the homologue in plant cells of the animal Golgi apparatus. Since it is these bodies which are most regularly impregnated—in some cases they are the only elements to be blackened—the osmic methods are particularly to be recommended for attempting their specific demonstration and further analysis.

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Explanation of plate 1

All of the figures have been outlined as far as possible with the camera lucida at an initial enlargement of approximately 1675 diameters, and subsequently completed free-hand. In reproducing, the figures have been reduced uniformly to an enlargement of approximately 1250 diameters. With the exception of fig. 1, all of the figures are printed with that side of the cell at the top which was originally directed toward the seed (or bulb). The method employed in the preparation of the original object is appended to the explanation of each figure.

Fig. 1. Osmiophilic platelets (blackened rings or rods) in a group of early androgonia from an antheridium of *Polytrichum commune*. Kolatchev method, variation IIb, 6 days.

Fig. 2. Osmiophilic platelets, from root-tip meristem of *Vicia Faba*. Kolatchev method, variation Ia, 8 days.

Fig. 3. Osmiophilic platelets (delicate, blackened rings) and plastidome (heavily blackened, elongate bodies), from root-tip (plerome-periblem border) of *Vicia Faba*. Kolachev method, variation IIb, 7 days.

Fig. 4. Osmiophilic platelets (delicate rings or rods), plastidome (heavily blackened, spheroidal bodies), and vacuome (faintly blackened, above and below the nucleus), from root-tip (plerome) of *Vicia Faba*. Kolatchev method, variation IIb, 6 days.

Fig. 5. Osmiophilic platelets and plastidome (heavily blackened bodies), from root-tip (root-cap) of *Pisum sativum*. Weigl method, 4 hour fixation, 9 days at 25°C.

Fig. 6. Plastidome, from old root-tip cell of *Pisum sativum*. Kolatchev method, variation Ia, 7 days.

Fig. 7. Plastidome (delicate threads) and pseudochondriome (intensely blackened granules), from root-tip (plerome) of *Hyacinthus orientalis*. Kolatchev method, variation IIb, 7 days.

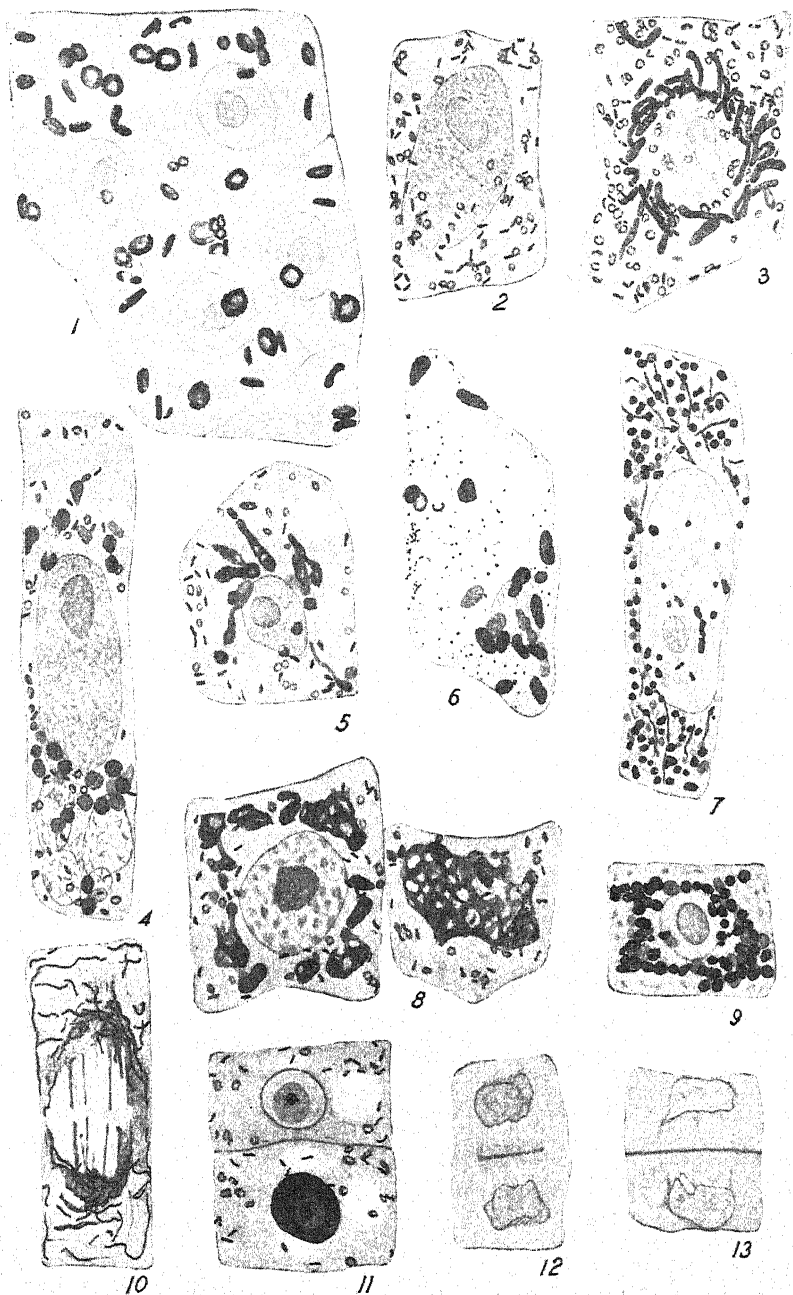
Fig. 8. Osmiophilic platelets and vacuome (blackened net-works), from root-tip (periblem) of *Vicia Faba*. Weigl method, 2 hour fixation, 6 days at room temperature.

Fig. 9. Vacuome (heavily blackened), from root-tip (periblem) of *Ricinus communis*. Weigl method, 1 hour fixation, 6 days at 25°C.

Fig. 10. Cytoplasmic fibrillae, metaphase, from root-tip (plerome) of *Pisum sativum*. Kolatchev method, variation Ia, 5 days.

Fig. 11. Osmiophilic platelets (delicate rings or rods) and nucleolar impregnations, from root-tip (periblem) of *Ricinus communis*. Kolatchev method, variation Ib, 6 days.

Figs. 12, 13. Cell-plate (telophases), from root-tip (plerome) of *Hordeum vulgare*. Weigl method, 4 hour fixation, 4 days at 25°C.



INDEX TO AMERICAN BOTANICAL LITERATURE 1926-1928

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Review, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Susceptibility of wheat to mildew as influenced by carbohydrate supply

SAM F. TRELEASE AND HELEN M. TRELEASE

Although the significant features in the nature of the host plant that determine its degree of susceptibility to disease are as yet very imperfectly understood, recent studies have shown that susceptibility of plants to parasitic disease may be profoundly influenced by environmental conditions, of temperature, moisture, light, mineral nutrient supply, etc. And in some cases valuable suggestions have been obtained regarding the manner in which the effective internal conditions of the host may be influenced. For a number of plant diseases caused by obligate parasites a general correlation exists in many cases between host vigor and susceptibility to disease—the more vigorous host being more susceptible to such diseases than the less vigorous host (Raines, 1922). Carbohydrate nutrition, in particular, has been found to have an important influence on the degree of susceptibility of the host to rusts and to mildews.

Fromme (1913) reported tests on the effect of light exclusion on the development of *Puccinia coronifera* on oats. Four cultures of the same age, seven days, were inoculated. One was placed in a darkroom and the other three were put in the greenhouse, in a glass box. After three days the first culture was transferred from the darkroom to the greenhouse. The incubation period for the three cultures kept in the greenhouse was eight days, while that of the culture left three days in the darkroom was eleven days. The difference of three days in the incubation period was exactly equal to the period of light exclusion and indicated a complete arrest of the development of the fungus in the darkroom. In another experiment, the effect of light exclusion during the latter part of the incubation period was tested. Four cultures were inoculated and placed in the greenhouse, in the glass box. Four days later one of them was transferred to the darkroom, where it was left four days, and then returned to the culture box. No signs of infection were visible on this culture at this time,

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while unripe pustules on the other cultures were plainly visible. The pustules on the cultures that remained in the greenhouse ripened on the ninth day, while three additional days, twelve days in all, were necessary for a similar development of the culture that had been in the darkroom. By excluding light four days in the latter part of the normal incubation period, maturation of the rust had been delayed three days. Thus, even after the fungus had become well established in the host, its development was strongly retarded in complete darkness. Fromme says that the retardation of the growth of the fungus may be the direct effect of total absence of light on the fungus itself. Or it is possible that the fungus simply suffers from lack of food, since the host is incapable of photosynthesis in darkness. He suggests, however, that it seems hardly possible that such a complete inhibition in the growth of the fungus should have resulted in the brief time involved unless the fungus is dependent on the transition products of photosynthesis. This latter possibility, he states, is by no means inconceivable, and should this explanation prove the correct one it could be made the basis for an explanation of the obligate parasitism of the rusts and their inability to develop on any form of artificial medium.

Reed (1914) studied the influence of light on infection of wheat and barley by mildews. Seedlings were grown in the dark until the first leaf was 2-3 cm. long and then inoculated with mildew spores from their respective hosts. Some of the inoculated plants were kept continuously in the dark and some were removed at once and placed in the light; at intervals of 24 hours other inoculated plants were transferred to the light. The general results were that no infection occurred if the plants were kept in the dark after inoculation. After removal of the seedlings to the light, infection occurred in proportion to the degree to which the etiolated leaves turned green. In general the period of incubation was retarded proportionally to the time the plants were kept in the dark. Another series of experiments was carried out, first growing the plants in the light and then, after inoculation, placing them in the dark, some immediately, others after intervals of 24 hours. In the case of the plants placed at once in the dark, no infection occurred. Those, however, that were kept in the

light for one or two days became infected. The period of incubation of the fungus, however, was materially retarded. Reed emphasizes the importance of chlorophyll, since he states that in general the effect of absence of light upon the mildew is considered to be an indirect one and has to do with the primary effect upon the development of chlorophyll in the host cell. The infection fails to occur, he says, in those cells which have not developed the chlorophyll. The mildew, according to Reed, is a strict parasite, not attacking cells which are not capable of carrying on their normal functions. These results, he says, are quite different from those obtained by inoculating etiolated plants with saprophytic fungi; under such conditions, in some cases at least, saprophytic fungi are able to develop on the living tissues.

Mains (1917) has reported experiments on the effects of light and carbohydrate supply upon the development of *Puccinia Sorghi* on maize and *Puccinia coronata* on oats. He found that when leaves or seedlings were first deprived of carbohydrates, light was necessary for the development of these parasites on their hosts since it is necessary for the formation of carbohydrate by the hosts. When the host was able to obtain a supply of carbohydrates from a solution, light was not necessary for the development of either parasite. The development of *Puccinia Sorghi* was checked when the host was deprived of carbon dioxide. Pure cultures of *Puccinia Sorghi* were maintained upon sterile seedlings and upon pieces of maize leaf floated upon solutions of starch, sucrose, dextrose, maltose, and dextrin in the dark. Development of the fungus did not occur unless a carbohydrate was present in the solution. Mains considers that the obligate parasitism of the rusts may probably be explained by their requirement of some transitory or nascent organic products, related to the carbohydrates, which they secure in the living host.

Leach (1919) has used specific food requirements of fungi as the basis of an hypothesis to explain the phenomena of rust resistance and biologic specialization in rusts. He considers that each biologic form of rust requires a specific food, which is produced only in a limited number of host forms.

The study here reported was planned in order to obtain

further information concerning the effect which carbohydrate supply might have upon the susceptibility of the host to parasitic disease. Wheat mildew was selected as representing a disease that could be readily studied under greenhouse and laboratory conditions.

INFLUENCE OF LIGHT UPON SUSCEPTIBILITY

Effect of period in dark after inoculation upon incubation period. The data recorded in table 1 were obtained in tests made to determine the effect of the length of an initial period in darkness upon the incubation period of wheat plants inoculated with mildew (*Erysiphe graminis*). Seedlings of Leap's Prolific (winter) wheat were grown in a shaded greenhouse for seventeen days in four-inch pots, about fifty seedlings in a pot. The seedlings, which were about 18 cm. high and had two expanded leaves, were sprayed with distilled water and inoculated at 5 o'clock in the afternoon with mildew spores shaken from heavily infected plants. Three similar tests were made. In the first test inoculation occurred on July 26, 1927; in the second, on August 2, 1927; and in the third on June 11, 1928. In the third test the plants were kept in darkness for two days preceding inoculation, in order to allow exhaustion of surplus carbohydrate from the leaves.¹ For each test eight lots, as shown in table 1, of two pots each were used. Immediately after inoculation, the first lot was left in the greenhouse where it was exposed to the usual alternating periods of light and darkness; the others were placed in the dark, and one lot was removed to the greenhouse each day. The darkroom is adjacent to the greenhouse and receives a continuous supply of fresh air from the latter, by means of an electric fan; thus temperature (averaging about 25°C.) and humidity were nearly the same in the greenhouse and in the darkroom. Observations were made twice daily, at 9 A.M. and at 5 P.M.; and a record was obtained of the approximate time when spore tufts became visible on the leaves.

No development of mildew spores occurred on inoculated plants left for 7 days or longer in the dark; these plants were very chlorotic and died a few days after being placed in the

¹ Wheat leaves, even after exposure to bright light, appear to have only a small excess of carbohydrate food. See a later section of this paper.

greenhouse. After the plants had been in the dark for about 4 days, numerous light yellow flecks appeared on the leaves, indicating initial infection, but spore masses did not develop on these plants. The lack of susceptibility of wheat in the dark suggests at once, as was pointed out by Fromme (1913), Reed (1914), and Mains (1917), that the leaves are not susceptible unless they contain an adequate supply of carbohydrate foods, normally manufactured in the light by photosynthesis.

TABLE 1

Effect of period in dark after inoculation upon incubation period (time required for mildew appearance)^a

PERIOD IN DARK, DAYS	INCUBATION PERIOD, DAYS				DELAY: INCUBATION PERIOD MINUS MINIMUM INCUBATION PERIOD, DAYS				PERIOD IN GREENHOUSE BEFORE MILDEW APPEARANCE, DAYS				PERIOD IN DARK MINUS DELAY, DAYS			
					1	2	3	Av.								
0	3.5	4.0	3.0	3.5	0.0	0.0	0.0	0.0	3.5	4.0	3.0	3.5	0.0	0.0	0.0	0.0
1	3.5	4.5	3.5	3.8	0.0	0.5	0.5	0.3	2.5	3.5	2.5	2.8	1.0	0.5	0.5	0.7
2	4.0	4.5	3.5	4.0	0.5	0.5	0.5	0.5	2.0	2.5	1.5	2.0	1.5	1.5	1.5	1.5
3	5.0	5.0	4.0	4.7	0.5	1.0	1.0	0.8	2.0	2.0	1.0	1.7	2.5	2.0	2.0	2.2
4	5.5	5.5	5.0	5.3	2.0	1.5	2.0	1.8	1.5	1.5	1.0	1.3	2.0	2.5	2.0	2.2
5	6.5	6.5	7.0	6.7	3.0	2.5	4.0	3.2	1.5	1.5	2.0	1.6	2.0	2.5	1.0	1.8
6	7.5	8.5	8.0	8.0	4.0	4.5	5.0	4.5	1.5	2.5	2.0	2.0	2.0	1.5	1.0	1.5

^a No infection occurred on plants left for 7 or 8 days in the dark; these plants were very chlorotic and died a few days after being placed in the light.

In the first test recorded in table 1 an initial period of 1 day in darkness did not lengthen the incubation period, but in the second and third tests it increased the incubation period by 0.5 day. Progressively longer periods in the dark definitely lengthened the incubation period. The delay in the appearance of mildew spores (actual incubation period minus minimum incubation period) varied directly with the length of the initial period in the dark.

The time required in the greenhouse before the appearance of mildew spores was less for the plants that had been in the dark than for those left in the greenhouse. Thus, tufts of mildew spores usually appeared in from 1.0 to 2.5 days after the plants were transferred from the darkroom to the greenhouse, whereas the minimum incubation period for plants remaining in the greenhouse was from 3.0 to 4.0 days. This indicates tha

spore germination and some development of mycelium occurred in the dark. That absence of light did not completely arrest the development of the mildew is also shown by the last four columns of table 1. When the plants were kept in the dark for one or more days, the delay in mildew appearance was never as great as the period during which the plants had been in darkness.

Injurious effects of darkness and of mildew upon wheat.

Some of the effects of mildew and of absence of light were observed after the plants were transferred from the darkroom to the greenhouse. These may be illustrated by a description of the appearance of the plants four days after the last culture had been removed from the darkroom. The plants were arranged in a series according to the length of their period in darkness, beginning with those that had not been in the darkroom after inoculation and ending with those that had remained for 8 days in the darkroom. This series represented progressively greater dwarfing, increased chlorosis, more pronounced drooping, and less abundant development of mildew. The plants which had been in the dark from 0 to 2 days were large and vigorous, dark green in color, erect, and heavily covered with tufts of mildew spores. Those which had been in darkness from 3 to 5 days were dwarfed (about three-fourths as tall as the preceding), increasingly chlorotic and wilted, and only sparsely covered with mildew conidia. And those which had been in the dark from 6 to 8 days showed greater dwarfing (being about one-half as tall as the plants not placed in the darkroom), they were extremely chlorotic, and they exhibited pronounced drooping. Only a very slight development of mildew spores was visible on the plants which had been in the dark for 6 days, and none on those which had been in darkness for 7 and 8 days.

Aside from showing the influence of darkness in rendering the plants less susceptible to mildew, these tests bring out the high degree of injury that results from exclusion of light. In fact, wheat plants seem to be injured more rapidly by darkness than by mildew. Seedlings are unable to survive a period of seven days in the dark, whereas they usually are able to live for two or three weeks with the most severe infection possible with mildew if other conditions are favorable.

These tests illustrate a difficulty met in attempting to correlate host vigor and susceptibility. The plants that were left in the greenhouse after inoculation were much more vigorous than those kept in the dark for 6 days, and, judging by their ability to support the fungus, they were much more susceptible to mildew. And yet the greater vigor of these plants enabled them to live considerably longer than the less susceptible plants that had been injured by lack of light. As time went on, the plants tended more and more to recover from the injury they sustained during the absence of light, but concurrently the injurious effects of the mildew infection became increasingly greater. Where two sets of adverse conditions have been operative together (here darkness and mildew infection), it may be difficult to evaluate the relative degree of injury that has been produced by either one of the conditions in question.

TABLE 2

Effect on mildew infection of placing inoculated plants in darkness after various initial periods in light^a

INITIAL PERIOD IN LIGHT, DAYS	INCUBATION PERIOD, DAYS	
	PLANTS	CUT LEAVES ^b
0	c	c
1	c	c
2	3.5	3.0
3	3.0	3.0

^a At beginning of test (June 24, 4 P.M.), the plants had been in the dark for 3 days; they were 12 days old, 19 cm. high.

^b When potted plants were placed in the dark, six leaves were cut off and placed on wet blotting paper in a moist chamber.

^c No infection occurred.

Effect on mildew infection of placing inoculated plants in darkness after various initial periods in light. Table 2 shows the results secured in a test made to determine the incubation period for plants that were inoculated and kept in the greenhouse for different periods of time and then transferred to the darkroom. The seedlings were grown in the greenhouse, and three days before inoculation they were put in the darkroom, so as to diminish the reserve carbohydrate food that they might contain. They were inoculated with mildew in the

greenhouse at 4 P.M. on June 24, 1928, when they were 12 days old and about 19 cm. high. The first set was placed immediately in the dark, the second was put in the dark after 1 day, the third after 2 days, and the fourth after 3 days. Duplicate pots, of about 50 seedlings each, were used for each treatment. When each set of plants was transferred to the dark, six leaves were cut off and placed on wet blotting paper in a moist chamber.

It will be seen from table 2 that no mildew developed on the plants placed immediately in the dark nor upon those left in the greenhouse for one day. But spores appeared after 3.5 days on the plants that remained in the greenhouse for 2 days before removal to darkness. This indicates that sufficient food—probably carbohydrate, protein, or both—was made or accumulated during the 2-day period to render the plants sufficiently susceptible to allow subsequent development of the parasite; secondary infection did not occur in the dark, however, and these plants died after about 12 days. The incubation period for mildew on the seedlings in the greenhouse was 3.0 days.

It is interesting to note that mildew spores may be formed sooner on cut leaves than on those remaining attached to the plant. This is seen in the case of the seedlings that had been in the greenhouse for 2 days before being transferred to the darkroom. The shorter incubation period was probably due to a greater retention of food by these leaf portions, since translocation was prevented by detachment from the basal growing region of the leaf as well as from the rest of the plant.

Slight development of mildew in dark on very young seedlings still receiving carbohydrate supply from endosperm. The tests thus far described were made with seedlings that had exhausted the carbohydrate of the endosperm and had been in darkness for a period of 2 or 3 days prior to inoculation (except in two tests recorded in table 1). In view of Mains's (1917) observation that the endosperm of maize continued for a long time to supply materials that allowed the development of rust in the dark, it seemed of interest to test the susceptibility of very young wheat seedlings that were still receiving food from the endosperm and had been carrying on

photosynthesis. For this purpose, seedlings that were only 4 days old, with the first green leaf about 8 cm. long, were inoculated at 4 P.M. on June 24, 1928, and placed immediately in the darkroom. At the end of four days a very slight development of small patches of mildew spores was visible on the leaves. Three days later, when the tufts had reached their maximum size, the amount of mildew was very small in comparison with the development on similar seedlings in the greenhouse.

Mildew development as an index of photosynthetic activity. The foregoing experiments, of course, suggest that the capacity of the wheat leaf to support the development of mildew might be used as an index of photosynthetic activity. This might prove useful for qualitative tests comparable to those of starch accumulation or increase in dry weight of the leaf.

INFLUENCE OF CARBOHYDRATE AND ALCOHOL SOLUTIONS
UPON SUSCEPTIBILITY OF LEAVES IN
DARKNESS

It has long been known that green leaves which have previously been freed from starch can absorb various organic substances from solution and form starch in the dark. The literature contains reports of many studies made to determine the species of plants in which starch formation may occur in darkness, the kinds and concentrations of organic substances that may be assimilated, and the effects of temperature and poisons on the process. Reference may be made here to the following workers who have made important investigations of these problems: Boehm (1883, 1889), Schimper (1885), E. Laurent (1886), Meyer (1886), Bokorny (1888), Acton (1889), Saposchnikoff (1889), Nadson (1890). Mazé (1899, 1911), J. Laurent (1904), Molliard (1907), Ravin (1913), Knudson (1916), and others have developed methods for growing green plants in sterile cultures and supplying them with organic substances through their roots.

Mains (1917) was able to grow pure cultures of *Puccinia Sorghi* upon sterile seedlings of maize and upon pieces of maize leaf floated upon solutions of starch, cane sugar, dextrose, maltose, and dextrin in the dark. The fungus did not develop upon either seedlings or pieces of maize leaf that

were exhausted of carbohydrates and supplied only with a salt solution or distilled water in the dark.

The foregoing studies suggested that wheat leaves kept in the dark might be susceptible to mildew if they were supplied with solutions of organic substances. Tests were therefore made to determine the effects of different kinds and concentrations of carbohydrate and alcohol solutions.

Effects of different kinds of carbohydrates and alcohols upon the development of mildew on wheat leaves in darkness. Seedlings of Leap's Prolific wheat were grown for fourteen days in four-inch pots, or until they were about 18 cm. high. After they had been placed in the dark for 2 days, to free them from a surplus of food, they were inoculated in the same manner as in the preceding tests. About 10 cc. of solution were poured into an ordinary Pyrex test-tube (150 mm. high and 18 mm. in diameter, without lip; capacity 30 cc.), and the test-tube was lightly plugged with absorbent cotton. The solutions were prepared with tap water, tests having shown that the development of the mildew was the same when tap water or distilled water was used. Three leaves were cut from the inoculated plants and quickly transferred to the test-tube. Each leaf portion, about 8 cm. long, floated in the solution, so that the cut end was submerged to a depth of about 2 cm. while the rest was exposed to the air within the test-tube. For each solution five test-tubes containing leaves were prepared and placed in the darkroom at an average temperature of about 21°C. The development of mildew on the leaves was observed by turning on an electric lamp for a few minutes, and final records were usually obtained after about seven days. No special precautions were taken to assure sterility of the preparations, but the mildew generally developed more rapidly than bacteria and other fungi, and the results were discarded where serious contamination occurred.

Table 3 shows the results secured with fourteen different carbohydrates and two alcohols. All of the solutions were prepared so as to have a carbon concentration equivalent to that of a 0.1 M dextrose solution. The various types of solutions differed in osmotic value, but the latter was never high enough to bring about injury to the leaves. Each of the fourteen carbohydrates and the two alcohols rendered the

leaves susceptible to mildew. Only a very few small spore tufts, hardly visible without the aid of a hand-lens, were formed on the control leaves supplied with tap water. Although exact estimation was not possible, the number of spores produced on the control leaves appeared to be less than one-hundredth as great as on the leaves marked in the table with a single *plus* sign.

TABLE 3

Development of mildew on leaves of wheat kept in darkness and supplied with solutions of carbohydrates and of alcohols; every solution prepared with tap water and equivalent in carbon concentration to a 0.1 M dextrose solution^a

GENERAL CLASS	SUBSTANCE	DEVELOPMENT OF MILDEW
Monosaccharides	Arabinose [$C_5H_{10}O_5$]	+
	Xylose [$C_5H_{10}O_5$]	++
	Rhamnose [$C_6H_{12}O_5 \cdot H_2O$]	+
	Dextrose [$C_6H_{12}O_6 \cdot H_2O$]	+++
	Levulose [$C_6H_{12}O_6$]	+++
	Galactose [$C_6H_{12}O_6$]	++
	Mannose [$C_6H_{12}O_6$]	+
Disaccharides	Sucrose [$C_{12}H_{22}O_{11}$]	+++
	Maltose [$C_{12}H_{22}O_{11} \cdot H_2O$]	++
	Lactose [$C_{12}H_{22}O_{11} \cdot H_2O$]	++
Trisaccharides	Melezitose [$C_{18}H_{32}O_{16} \cdot 2H_2O$]	+++
Non-sugars	Starch [$(C_6H_{10}O_5)_n$]	+
	Dextrin [$(C_6H_{10}O_5)_n$]	+
	Inulin [$(C_6H_{10}O_5)_6 \cdot H_2O$]	+
Alcohols	Glycerine [$C_3H_5(OH)_3$]	++
	Mannite [$C_6H_8(OH)_6$]	+

^a Only a few, extremely small tufts of spores developed on the control leaves, inoculated with mildew and supplied with tap water. Number of spores produced on these control leaves appeared to be less than one-hundredth as great as the number on leaves marked +.

The roughly quantitative comparison recorded in table 3 shows that the monosaccharides dextrose and levulose, the disaccharide sucrose, and the trisaccharide melezitose were most effective in increasing the susceptibility of the leaves to mildew. The monosaccharides xylose and galactose, the disaccharides maltose and lactose, and the alcoholglycerine

appeared to be less effective. And the monosaccharides arabinose, rhamnose, and mannose, the non-sugars starch, dextrin, and inulin, and the alcohol mannite seemed to be least effective. The reasons for these differences may be expected to depend upon a complex set of conditions, involving the rate of diffusion of the organic substance in question, the ability of the leaf cells to absorb the substance directly or after digestion by enzymes,² the rate of translocation of the substance or of its products from the subepidermal to the epidermal cells of the leaf, the capacity of the leaf cells to convert the substance into forms that can be used by the parasite, etc. The action of the organic substance may in some cases involve injurious chemical and osmotic effects upon host and parasite. Since the branched haustoria of the mildew penetrate only the epidermal cells (Smith, 1900), it is obvious that the growth of the fungus should be markedly influenced by the kinds and concentrations of substances within these cells.

All of the substances listed in table 3 are utilized by fungi and bacteria in artificial culture, and many of them induce the accumulation of starch in leaves supplied with them in darkness. By hydrolysis, of course, sucrose is converted into dextrose and levulose; maltose into dextrose; lactose into dextrose and galactose; melezitose into dextrose and turanose (isomeric with sucrose) and the latter into dextrose and levulose; starch into dextrin and maltose and the latter into glucose; and inulin into levulose. Little is known, however, concerning the nature of the chemical alterations which they undergo during utilization by fungi or by green leaves.

It is interesting to note in this connection that when leaves are supplied with sucrose solutions in the dark, there is an increase in the protein content of the leaves (Saposchnikoff, 1889, 1890, 1891, 1893), and proteins thus formed may be of importance in rendering wheat leaves susceptible to mildew. Although most fungi that can be grown in artificial culture are able to elaborate their own proteins from carbohydrates and simple mineral salts, sufficient evidence is not yet available to show how important a part the proteins of the host may

² It would be expected that absorption of colloidal starch could occur only after extracellular digestion, such as takes place in cultures of fungi or bacteria growing in starch media.

have in the development of obligate parasites. From present knowledge, it would not be safe to assume that the degree of susceptibility of wheat to mildew is simply a question of the kinds and concentrations of carbohydrates present in the wheat.

Fromme (1913), in attempting to explain the retardation of growth of oat rust on its host in the dark, suggests that the fungus may be dependent on the transition products of photosynthesis. The present tests indicate that mildew development may depend just as well upon products of digestion as upon products of photosynthesis. And it is apparent that many different carbohydrates, as well as glycerine and mannite, may furnish the wheat leaf with materials which, directly or indirectly, allow the fungus to derive nourishment.

The obligate parasitism of the rusts might be explained, according to Fromme (1913), by their dependence upon transition products in photosynthesis, or similarly, according to Mains (1917), by their requirement of some transitory or nascent organic products (certain stereoisomers, possibly) related to the carbohydrates, which they obtain only in the living host.

Specific food requirements of fungi have been found in many cases since Pasteur's original discovery of the action of *Penicillium glaucum* on dextro-, levo-, and racemic-tartric acid.

Leach (1919) has elaborated an hypothesis to explain the phenomena of rust resistance and biologic specialization in rusts. He supposes that each biologic form of rust has its specific food requirements, conforming with the molecular configuration of its protoplasm. This food, which is in turn specific in relation to the protoplasm which produces it, is found only in a limited number of host species. When a given biologic form of rust invades a plant that does not contain this specific food, the fungus consequently dies of starvation and in this process of starvation secretes an enzyme that is injurious to the plant cells with which it comes in contact.

Experimental evidence is not yet available concerning the forms of food directly utilized by the rusts or by the mildews. It is clear, however, that the proper transformation of any one of many carbohydrates, as well as of glycerine and mannite,

occurs readily in the wheat leaf so that the required foods are supplied to the mildew. It is obvious, of course, that the reason why wheat is often susceptible to wheat mildew while barley is always immune to this fungus cannot be explained in terms of carbohydrate *content* (since both wheat and barley may have the same amount); but it might possibly be explained, as suggested by Leach, in terms of the *kind* of carbohydrate—no two plant species having exactly the same kind of starch, protein, etc.

TABLE 4

Development of mildew on leaves of wheat kept in dark and supplied with various concentrations of sucrose in tap water

CONCENTRATION		DEVELOPMENT OF MILDEW
Relative carbon concentration ^a	Grams per 100 cc. of solution	
0	0	0 ^b
1/512	0.003	0 ^b
1/256	0.007	0 ^b
1/128	0.013	0 ^b
1/64	0.027	0 ^b
1/32	0.053	0 ^b
1/16	0.107	0 ^b
1/8	0.214	+
1/4	0.428	+
1/2	0.855	+
1	1.711	+++
2	3.422	++++
4	6.844	+++++
8	13.687	++++++
16	27.374	+++++++

^a Ratio of carbon concentration to carbon concentration of a 0.1 M dextrose solution.

^b Only a few, extremely small tufts of spores produced.

Effects of the concentration of sucrose, dextrose, and glycerine upon the development of mildew on wheat leaves in darkness. The results recorded in tables 4–6 were obtained in tests made to determine effects of different total concentrations of sucrose, dextrose, and glycerine upon the susceptibility of wheat leaves to mildew in darkness. In tables 4 and 5 the concentrations are expressed as relative values in which unity

represents a carbon concentration equivalent to that of a 0.1 M dextrose solution. In table 6 the concentrations are given in terms of osmotic value.

Only a few, extremely small tufts of mildew spores, generally visible only with the aid of a hand-lens, appeared on the leaves supplied with tap water alone. This development was so slight that it is recorded as zero in attempting to estimate the relative abundance of spores on the leaves (table 4). Relative concentrations of sucrose from 1/512 to 1/16 appeared to be no more effective in increasing the susceptibility of the leaves. But a clear increase in spore production was evident with relative concentrations of 1/8, 1/4, and 1/2; and increasingly higher concentrations gave greater development. The optimum concentration was not exceeded, since the highest concentration (16, or 27.374 grams of sucrose per 100 cc. of solution) allowed the most abundant production of spores.

In the tests recorded in table 5 an attempt was made to estimate more accurately the relative abundance of mildew that developed on leaves supplied with a series of concentrations of sucrose, dextrose, and glycerine. The preparation showing the greatest development of spores per unit leaf area was assigned a value of 100, and indices were given to the other preparations by comparison with this standard. Development of mildew in the tap water controls was extremely slight. With the sucrose solutions the abundance of mildew increased rapidly as the concentration became higher, and an optimum is indicated for a relative concentration of 16. Spore production on leaves supplied with the optimum solution was much more abundant than was ever observed on cultures in the greenhouse. Similar results were obtained with dextrose solutions. The lower concentrations of dextrose appeared to give somewhat higher values than the corresponding concentrations of sucrose, the optimum was reached at a lower carbon concentration than with sucrose, and a marked falling off in mildew development occurred with the highest concentrations. The lower concentrations of glycerine seemed to be more effective than similar concentrations of either sucrose or dextrose; the optimum was attained at a carbon concentration of only 4, and a rapid decrease in mildew is evident for concentrations exceeding

the optimum. At its optimum concentration glycerine was only about 50 per cent as effective as sucrose at its optimum, and dextrose was about the same as sucrose.

The data of table 5 have been rearranged in table 6 to bring out the relation of the osmotic concentration of the solutions to the development of mildew in the dark. Approximate osmotic values were calculated by the formula $\pi = MRT$, in

TABLE 5

Development of mildew on leaves of wheat kept in dark and supplied with various concentrations of sucrose, dextrose, and glycerine in tap water

RELATIVE CARBON CONCENTRATION ^a	DEVELOPMENT OF MILDEW		
	Sucrose	Dextrose	Glycerine
0	0 ^b	0 ^b	0 ^b
1/32	1	1	1
1/16	1	1	1
1/8	1	1	2
1/4	1	1	3
1/2	5	3	4
1	10	20	10
2	20	40	40
4	70	70	50
8	90	90	20
16	100	45	5
32	50	10	1

^a Ratio of carbon concentration to carbon concentration of a 0.1 M dextrose solution. Thus, each of the following solutions has a relative carbon concentration of unity: 0.05 M sucrose, 0.1 M dextrose, 0.2 M glycerine.

^b Only a few, extremely small tufts of spores produced.

which π is the osmotic value in atmospheres, M is the volume-molecular concentration, R is the constant 0.082, and T is the temperature on the absolute scale (here considered to be 273 plus 21, or 294). The formula thus becomes $\pi = 24.1M$. In making these calculations, osmotic values are thus assumed to be directly proportional to volume-molecular concentrations. It is to be noted that for equivalent carbon concentrations the volume-molecular concentrations, and therefore the osmotic concentrations, are as 0.05:0.10:0.20 or as 0.5:1:2 for sucrose ($C_{12}H_{22}O_{11}$), dextrose ($C_6H_{12}O_6$), and glycerine ($C_3H_5(OH)_3$), respectively.

Examination of table 6 shows at once that the optimum osmotic value for mildew development is 19.28 atmospheres (or 0.8M) for each of the substances, although the relative carbon concentrations of the optimum solutions, as shown in the preceding table, are different—16 for sucrose, 8 for dextrose, and 4 for glycerine.³ This suggests that the optimum concentration for each substance is limited by the osmotic

TABLE 6

Relation of osmotic concentration of solutions of sucrose, dextrose, and glycerine to development of mildew on leaves of wheat in darkness

OSMOTIC CONCENTRATION, ATMOSPHERES ^a	DEVELOPMENT OF MILDEW		
	Sucrose	Dextrose	Glycerine
0	0 ^b	0 ^b	0 ^b
0.04	1	—	—
0.08	1	1	—
0.15	1	1	1
0.30	1	1	1
0.60	5	1	2
1.21	10	3	3
2.41	20	20	4
4.82	70	40	10
9.64	90	70	40
19.28	100	90	50
38.56	50	45	20
77.12	—	10	5
154.24	—	—	1

^a Calculated by formula $\pi = 24.1M$, in which π is the osmotic value in atmospheres and M is the volume-molecular concentration.

^b Only a few, extremely small tufts of spores produced.

properties of its solution, and may be related to serious injury through plasmolysis of leaf cells, to low water-supplying power of the solution, to high vapor-pressure deficit of the atmosphere above the solution, etc. A comparison of tables

³ The optimum sucrose solution contains 27.37 grams per 100 cc. of solution; the optimum dextrose solution 14.41 grams of the anhydrous sugar; and the optimum glycerine solution, 7.36 grams. These values represent approximately the percentages of solute. For accurate equivalents on the percentage basis (grams of solute per 100 *grams* of solution), the densities of the solutions would have to be known.

5 and 6 indicates that the increase in mildew development, below the optimum, is correlated more closely with the carbon concentration of the solution than with its osmotic concentration. Thus, for the lower concentrations the capacity of the solution to induce the development of the mildew on the wheat leaf seems to be largely determined by carbon concentration and to be nearly the same for different kinds of solutions equivalent in carbon concentration. But as the carbon concentration of a solution of any one of the substances is increased, the increase in effectiveness appears to reach a limit determined by osmotic properties. The optimum solutions of sucrose, dextrose, and glycerine gave indices of mildew development of 100, 90, and 50, respectively. These differences seem to be determined, in part at least, by the fact that without exceeding 19.28 atmospheres a relative carbon concentration of 16 may be obtained with sucrose, while the corresponding carbon concentrations obtainable with dextrose and glycerine are only 8 and 4, respectively.⁴

In general a given osmotic concentration of sucrose induced the production of more mildew than did the same osmotic concentration of dextrose, and the latter had a greater effect than glycerine (table 6). Solutions having the same osmotic value also have the same number of molecules per unit volume, but each molecule of sucrose contains twice as many atoms of carbon as a molecule of dextrose, and a molecule of the latter has twice as many as a molecule of glycerine. Thus, with solutions equivalent in molecular concentration, effectiveness in promoting mildew development appears to be directly related to the amount of carbon contained in each molecule.

The capacity of a solution of an organic substance to increase the susceptibility of the leaf to mildew may be expected to depend upon a very complex set of conditions.

⁴ In interpreting these results, it should of course be borne in mind that the optimum concentration for each substance might be determined more precisely by using a series of solutions with smaller gradations in concentration. In the series here employed, each solution has double the concentration of the preceding solution. Although the optimum osmotic concentration, as here determined, is 19.28 atmospheres, it should be recognized that the exact optimum might lie at a somewhat different concentration between 9.64 and 38.56 atmospheres.

The following conditions may be mentioned as important in this connection: (a) the power of the solution to supply organic material to the leaf (depending mainly upon the nature and molecular concentration of the dissolved substance), (b) the capacity of the leaf to absorb the organic substance in question, (c) the possible rate of conduction of the organic substance or its products to the epidermal cells, (d) the capacity of the leaf to transform the substance into materials that can be utilized by the fungus, and (e) the nature and degree of chemical and osmotic effects which the solution exerts upon host and parasite.

Only very small amounts of starch were found in uninfectd and infected wheat leaves supplied in the dark with solutions of sucrose, dextrose, or glycerine. Tests were made in the usual way, by placing leaves in boiling water for one minute, then in alcohol until decolorized, and finally in a weak solution of iodine in fifty per cent alcohol, with enough chloral hydrate to nearly saturate the solution. The leaves showed no blue coloration to the naked eye, and microscopic examination revealed only a very small number of starch grains, in the bundle sheaths. Wheat leaves from plants out-of-doors also contained no starch or only a very slight trace. The wheat plant apparently stores soluble carbohydrates as such and does not transform them into starch. Even the amount of soluble carbohydrate accumulated seems to be small under usual conditions with the leaf attached to the plant. Sugar analyses would be instructive in this connection.

The mineral nutrition of these wheat leaves did not appear to be a limiting factor in the ability of the leaves to support mildew in these experiments. Mildew development was found in preliminary tests to be nearly the same on excised leaves supplied with a number of different three-salt solutions containing sugar; and the results seemed to be the same when tap water or distilled water was used in preparing sugar solutions. Since the susceptibility of plants grown for longer periods in solution cultures may be markedly influenced by the composition of the solution (Trelease and Trelease, 1928), it may be expected that leaves in darkness may be found to differ in susceptibility if variations in mineral supply are sufficiently pronounced. The present study suggests, more-

over, that low susceptibility of plants grown in some culture solutions may result from an inhibition of the normal manufacture of carbohydrates in the leaves; this might occur, for example, when the culture solution contained toxic concentrations of salts of the heavy metals or when it contained the usual mineral nutrients in markedly unbalanced proportions.

Chlorophyll disappears rather rapidly from wheat leaves supplied with the various sugars in darkness, so that pronounced chlorosis is evident after from seven to ten days. Differences were observed, however, in the rate of chlorophyll disappearance from leaves receiving the various solutions, the most conspicuous difference being the longer retention of the chlorophyll in leaves supplied with glycerine. The green color also remained longer in leaves that were free from mildew—uninoculated leaves in carbohydrate solutions and inoculated leaves receiving only tap water or distilled water. Thus, mildew infection hastens the disappearance of chlorophyll from the leaf in the dark as well as in the light. Chlorophyll persisted longer in the neighborhood of mildew spore tufts than in other parts of the leaf. This is the so-called green-island phenomenon, widely observed and reported in the literature of the rusts (see especially Rice, 1927). Reed (1904) reported that cells of the infected areas of the rye leaf retained their green color for a longer time than the other cells, while the reverse was true for the blue-grass leaf.

When the spores were scraped from leaves kept in the dark a new tuft of spores developed in one or two days. Spores continued to be produced for more than a week, until the leaves gave every external indication of being dead. Thus, the process appeared to be like that occurring in infected leaves in the greenhouse.

That chlorophyll is unnecessary for the development of mildew in the dark was clearly shown by a test with etiolated leaves, made at the same time as the tests recorded in tables 5 and 6 and with seedlings of the same age but grown in the dark. The leaves lacking chlorophyll were treated in the same manner as the green leaves and were supplied with sucrose and dextrose solutions, each with a relative carbon concentration of 4. Mildew developed as rapidly and as abundantly on these leaves as on those which contained chlorophyll.

INFLUENCE OF CARBOHYDRATE SOLUTIONS UPON
SUSCEPTIBILITY OF LEAVES DEPRIVED
OF CARBON DIOXIDE

It would be expected from the preceding experiments and from Mains's (1917) study of rusts that wheat leaves deprived of carbon dioxide would not be susceptible to mildew, even in the light, unless a suitable carbon compound were supplied to the leaves. This was readily demonstrated by the test described below.

Wheat plants, about 18 cm. high, were placed in the dark for two days so that most of their surplus carbohydrate food would be exhausted. The plants were then sprayed with distilled water and heavily inoculated with mildew spores. Three leaves were removed and placed with their cut ends in tap water in a small vial, and the vial was suspended in a two-quart Mason jar. A wire passed around the neck of the vial, and a loop in the upper end hung on a hook inserted in a paraffined cork stopper that closed the mouth of the jar. The cork bore a straight calcium-chloride tube with a vial suspended about its lower end. This tube was filled with small pieces of pumice stone. The jar contained tap water to a depth of about 2.5 cm. A second jar was arranged with pieces of potassium hydroxide mixed with pumice in the calcium-chloride tube, and with potassium hydroxide solution (120 grams of KOH in 400 cc. of water) replacing water in the bottom of the jar. A third jar was similar to the second except that a 3 per cent sucrose solution (relative carbon concentration, 1.75) was used instead of tap water in the vial holding the leaves. All three jars were placed in a north window of the laboratory.

The first chamber thus contained ordinary air. The second and third contained air lacking carbon dioxide. The leaves in the first two chambers received tap water, while those in the third chamber were supplied with a carbohydrate solution.

Well developed tufts of mildew spores appeared after five days on the leaves in the first and third jars; no spores were visible on the leaves of the second jar, even after ten days.

This experiment shows that development of mildew spores does not occur on leaves exposed to light and kept in an atmosphere free from carbon dioxide, but that the leaves may be-

come susceptible if supplied with a solution containing a suitable carbon compound.

DISCUSSION

Conditions determining the susceptibility of wheat to mildew. The results of the present study show that the susceptibility of the wheat leaf to a given strain of mildew was promoted by conditions which led to the accumulation of surplus carbohydrate in the leaf. Although it may be inferred that the degree of susceptibility was here controlled by carbohydrate content, sufficient information is not available to show whether the carbohydrates themselves, or whether other substances (proteins, etc.), whose formation is dependent on carbohydrates, are directly influential in determining susceptibility. The term susceptibility is used in a broad sense to denote the summation of the conditions within the host that tend to facilitate injury by the parasite. And the criterion of susceptibility here employed is the relative abundance of mildew spores developed per unit area on a number of different leaves, which had previously been equally inoculated with mildew spores and then kept under conditions tending to assure uniform pathogenicity of the parasite.

It may be expected that many complex conditions operate together in determining the degree of susceptibility of a particular host to a given parasite. The relative quantitative significance of the various component conditions may be very different in different cases. Thus, it is conceivable that morphological conditions, nitrogen content of the host cells, water content, hydrogen-ion concentration, concentration of certain substances that are poisonous to the parasite, kinds and concentrations of carbohydrates, proteins, fats, enzymes, pigments, etc., may each exert a preponderating influence in certain cases. With the general conditions involved in the present study, susceptibility of the wheat leaf to a certain strain of mildew appears to be proportional to the carbohydrate content of the epidermal cells of the host.⁵ It therefore

⁵ Failure of the host to supply the fungus with adequate food materials seems to be the simplest explanation of the low susceptibility of leaves lacking a carbohydrate excess. Other important features may, of course, be correlated with low food content—substances poisonous to the fungus may be produced most abundantly in host cells inadequately supplied with carbohydrate food,

seems worth while in this connection to summarize briefly the conditions that determine the carbohydrate content of the epidermal cells into which the parasite grows.⁶ The carbohydrate content of the epidermal cells at any particular time may be considered to depend upon the following conditions:

- I. Past rates and periods of processes tending to increase carbohydrates in epidermal cells, depending upon:
 - A. Rates and periods of entrance of carbohydrates into epidermal cells, depending upon:
 - a. Carbohydrate content of subepidermal cells, depending upon:
 1. Rates and periods of processes tending to increase carbohydrate in subepidermal cells, depending upon:
 - (A) Rates and periods of entrance of carbohydrates from outside the cells (as from endosperm, from other parts of plant, or from carbohydrate solutions supplied to leaf).
 - (B) Rates and periods of formation of carbohydrates in these cells:
 - (a) By photosynthesis, depending upon:
 - (1) Quality and intensity of absorbed light.
 - (2) Carbon dioxide absorption.
 - (3) Temperature.
 - (4) Chlorophyll content.
 - (5) Water content.
 - (6) Concentrations of products.
 - (7) Condition of protoplasm (dependent on the nature of the plant and on the sum total of previous physical and chemical conditions or stimuli).
 - (b) By other physiological processes (usually a negligible factor).
 2. Rates and periods of processes tending to decrease carbohydrates in subepidermal cells, depending upon:
 - (A) Rates and periods of exit of carbohydrates (by translocation, to epidermal cells, out of leaf, etc.).
 - (B) Rates and periods of decomposition of carbohydrates (by respiration, protein formation, assimilation of protoplasm, etc.).

or such cells may be most readily killed (hyper-sensitive) and thus lead to death of haustoria. Low protein content of the host cells, generally associated with deficient carbohydrate supply, may be an important condition in determining low susceptibility.

⁶ It is of course realized that this outline is tentative and incomplete, and that even the relations which the outline attempts to indicate might be shown by a number of other schemes.

- b. Rates and periods of movement of carbohydrates from sub-epidermal to epidermal cells.
- B. Rates and periods of formation of carbohydrates within epidermal cells, by photosynthesis in stomatal guard cells and by transformation of various organic compounds in epidermal cells.
- II. Past rates and periods of processes tending to decrease carbohydrates in epidermal cells, depending upon:
 - A. Rates and periods of movement of carbohydrates out of epidermal cells (by movement into other host cells and into fungus haustoria).
 - B. Rates and periods of decomposition of carbohydrates (by respiration, protein formation, assimilation, etc.).

Absence of disease under conditions of high susceptibility of the host. Since the actual development of disease depends not only upon the susceptibility of the host but also upon the pathogenicity of the parasite, sets of influential conditions may exist in which no development of the disease occurs in spite of high susceptibility of the parasite and heavy inoculation with mildew spores (see discussion by Trelease and Trelease, 1928). This appears to be the explanation of the usual absence of wheat mildew on plants growing out-of-doors in full sunlight.

Duggar (1909) states that wheat under partial shade often is badly infected with powdery mildew, which in the central part of the United States is seldom, if ever, seen in the open. He also says that time and again, in that same region, one may observe that in the case of well-watered lawns the mildew of blue grass abounds in a circle rather sharply limited by the heavier shadow areas of trees. Butler (1918) states that wheat mildew in India has only been seen causing serious damage in half-shaded pot culture experiments.

These general observations were confirmed by tests made during the summer in full sunlight and under deep shade of trees near the Columbia University greenhouses. Inoculated plants kept in the shade always became heavily infected with mildew, while those in the open usually showed only a slight flecking of the epidermis and no development of spore tufts.

It appears probable that direct sunlight increases the rate of photosynthesis and therefore tends to increase the susceptibility of the host to mildew, but intense light seems also to inhibit the pathogenicity of the parasite, by direct

action or because of high evaporation and consequent drying of the mildew conidia and superficial mycelium. Thus, the actual development of the disease may be completely inhibited in spite of the high susceptibility of the host.

Observations on the relation of temperature to mildew development have indicated that the optimum temperature is about 20°C., and that practically no development of mildew occurs at 30°C. It is impossible as yet, however, to state to what degree the checking of the disease by high temperatures depends upon low pathogenicity of the parasite and to what degree it depends upon low susceptibility of the host (the latter possibly associated with low carbohydrate content as the result of high rates of respiration and low rates of photosynthesis). Reed (1916) observed that only very slight infection occurred on plants kept under bell-jars exposed to bright sunlight in a greenhouse that had not been white-washed. He attributed the low degree of infection to the high temperature within the bell-jar, but he did not determine the relative effects of temperature upon host and upon parasite.

SUMMARY

Wheat plants must be exposed to light in order to render them susceptible to mildew (as indicated by their capacity to support development of mildew and production of spores) under usual conditions. When infected plants were placed in the dark for one or two days and later removed to the light, the incubation period was nearly as short as for plants not put in the dark (about three and one-half days). When similar plants were placed in the dark from three to six days, the incubation period was lengthened by a period which was about two days less than the initial period in darkness. Plants left in the dark for seven or eight days were nearly dead at the end of this time, and no mildew developed on them.

Wheat leaves in darkness were susceptible to mildew and supported an abundance of conidia if they were supplied with a solution containing any one of many carbohydrates or with a solution containing glycerine or mannite. Only a few very small tufts of conidia appeared on similar leaves supplied with tap water containing no carbohydrate.

Chlorophyll is not necessary, since mildew developed

as readily on etiolated leaves in the dark as on green leaves, if a carbohydrate or glycerine was supplied to the leaves.

Salt nutrition was not a limiting factor under the conditions of these tests, since a carbohydrate solution made with distilled water was about as effective as such a solution made with tap water or with a nutrient salt solution.

The capacity of solutions of sucrose, dextrose, and glycerine to render leaves in the dark susceptible to mildew appears to be directly related to the carbon concentration of the solution. Susceptibility increased with increase in concentration until a limit was reached which apparently depends upon the osmotic properties of the solution, this limit being about 19 atmospheres for each of the three substances.

Leaves exposed to light and kept in an atmosphere free from carbon dioxide were not susceptible to mildew unless they were supplied with a carbohydrate solution.

Leaves of very young plants, which were receiving a supply of carbohydrates and other materials from the endosperm, were slightly susceptible to mildew in darkness. Leaves detached from these plants and placed in tap water in darkness were also slightly susceptible.

All of the data secured in the present tests indicate that a relatively large surplus of carbohydrate in the host leaf is necessary for the abundant development of mildew; the supply of carbohydrate must be considerably greater than that required for retention of life by the leaf. Under usual conditions the carbohydrates may be transition products of photosynthesis, but they are not necessarily such products, since cut leaves may be rendered susceptible to mildew if supplied with a solution of glycerine or of any one of many carbohydrates.

The development of the mildew appears to be strictly limited by the life of the host. No tendency was observed for the mycelium to spread in the carbohydrate solution beyond the leaves. The green island phenomenon, moreover, suggests the very intimate and possibly even mutualistic relation between the host and the obligate parasite, and indicates that the development of the parasite is dependent upon the continuance of the host's metabolism.

In the present experiments, as well as in a series of tests

on the influence of mineral nutrition on susceptibility, no evidence was obtained which indicated that starvation or any other form of injury to the host favors the development of the mildew.

Although the present tests emphasize the need of more accurate criteria of health and vigor than are now available, a direct relation between general health or vigor of the wheat leaf and susceptibility to mildew seems to be suggested by these studies dealing with the carbohydrate nutrition of the leaf. That carbohydrates are significant not only as materials for assimilation but as sources of energy in protein synthesis is well established. The known facts and the probable relations of carbohydrates to the essential metabolic processes of both host and parasite point to the general conclusion that conditions which tend to lower the vigor of the host decrease the susceptibility of wheat leaves to mildew and conversely conditions which tend to favor the life processes of the wheat plant increase its susceptibility to mildew. This conclusion is in accord with the results of most workers on parasitic disease in plants and apparently contradicts sweeping statements, found in current treatises on animal pathology, regarding the direct relation of lowered vitality to susceptibility.

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New species of fossil plants from the Tertiary shales near De Beque, Colorado

ARTHUR HOLLICK

(WITH PLATE 2)

The three species here described and figured were included in a collection of about forty specimens transmitted to me for identification, in August 1928, by the Department of Public Education of the American Museum of Natural History.

Apparently two different floras were represented in the collection. One, which included about two thirds of the specimens, contained a number of species characteristic of the Florissant lake-bed deposits, such as *Celastrus fraxinifolius* Lesquereux, *Fagopsis longifolia* (Lesquereux) Hollick, *Lomatia* cf. *terminalis* or *tripartita* Lesquereux, *Myrica coloradensis* Knowlton, *Myrica drymeja* (Lesquereux) Knowlton, and *Rhus coriarioides* Lesquereux. These may be inferred to be of Oligocene or Miocene age. The other flora, included in the remainder of the specimens, contained several species typical of the Green River shales, such as *Aralia wyomingensis* Knowlton & Cockerell, *Myrica praedrymeja* Knowlton, and *Quercus castaneopsis* Lesquereux, which are Eocene in age, and others that represented undescribed species. Among the latter were the three that form the subject matter of this paper.

The collection, in its entirety, is recorded as having been made by Mr. Edmund Reynolds, at 'different altitudes', in the Tertiary oil shale beds in the vicinity of De Beque, Colorado. The probability appears to be that specimens from two different geological horizons are included in the collection; that the three specimens here described belong in the older one; and that this one represents the upper part (Bridger formation) of the Green River shales.

If fuller information should be desired in regard to the exact stratigraphic relations of the shales, the subject may be found critically and exhaustively discussed by Dr. F. H. Knowlton, in his 'Revision of the flora of the Green River formation, with descriptions of new species'¹.

¹ U. S. Geol. Survey, Prof. Paper 131-F (Shorter contributions to general geology. 1922), pp. 133-182. pl. 36-40. Mar. 30, 1923.

Pontederites thecoides n. sp. Organism apparently representing the remains of a membranous spathe, sheath, or bract-like leaf, 12 or more centimeters in length, expanded at one extremity to a width of about 2 cm., and contracted, for a distance of 3.5 cm. at the opposite extremity, to a width of about .75 cm.; nervation consisting of numerous closely approximated parallel veins, including a major series and an obscurely defined minor series between, the two series connected by numerous cross veinlets that subtend approximately right angles with their supporting veins, forming a fine quadrangular reticulation throughout. Museum New York Bot. Gard. No. $\frac{5.8}{3}$ (plate 2, fig. 1).

Numerous comparisons were made between this specimen and various parts of a number of existing species of monocotyledonous plants, without, however, arriving at satisfactory conclusions in regard to either its generic relationship or its morphologic status. It may be inferred, however, without question, that it belongs in the Monocotyledoneae, and its general appearance is suggestive of a flattened spathe or floral bract, or a clasping basal leaf or sheath common to certain plants such as are represented in the genus *Musa*, and in the genera *Pontederia*, *Piaropus*, etc., in the Pontederiaceae, and *Peltandra*, *Orontium*, etc., in the Araceae; but which is the distal and which the proximal extremity of the specimen I am unable to determine. The broader, disrupted part may have been spathe-like, originally; and the dark, irregular patches, that are conspicuous features where a portion of the membranous area is missing, are suggestive of some disintegrated enclosed organ, such as a spadix or flower cluster. On the other hand it also presents somewhat the appearance of a basal stem sheath, tubular and clasping below, open and flaring above. In the circumstances any more definite expression of personal opinion would appear to be of little value or interest.

Reference of the species to the genus *Pontederites* Knowlton² might, perhaps, be regarded as not entirely justified. The genus was based by the author on a disrupted fragment of what he inferred to be the apical part of a monocotyledonous leaf resembling those of *Pontederia cordata* Linnaeus. His figure shows indications of a midvein, which feature is not ap-

² Knowlton, F. H., *op. cit.*, p. 154, *pl.* 36, *fig.* 6.

parent in our specimen. Otherwise, however, the nervation appears to be mutually identical; and inasmuch as both specimens belong in one and the same geological horizon there would seem to be no inconsistency in relegating them to one and the same genus. They may, in fact, represent different organs of a single species—one a leaf, the other a spathe or sheath.

Odostemon Reynoldsii n. sp. Leaflet lanceolate-ovate in shape, coriaceous, about 5 cm. in length by 2.5 cm. in maximum width, tapering above, rounded below to a broad cuneate base, short petiolate; margin finely denticulate from the widest part of the leaflet upward, entire below; nervation pinnate, craspedodrome; secondary nerves irregularly spaced and disposed, subtending various angles with the midrib, flexed and angled, the angles connected by tertiary cross nervation, with ultimate fine nervilles extending to the marginal denticulations. Mus. New York Bot. Gard. $\frac{5.8}{2a}$ (plate 2, fig. 2).

Practically the only discernible difference between this specimen and many of the leaflets of existing species of *Odostemon* Rafinesque (= *Berberis* Linnaeus, and *Mahonia* Nuttall) is the fine marginal denticulation of the fossil as compared with the prevailingly coarser dentition in most of the existing species. Heterophylly, however, is a well marked character of the genus, and leaflets may be readily selected from individual plants that are strikingly similar to ours in form and in marginal features, especially in specimens of *Odostemon nutkanus* (DC.) Gaines, and *O. pallidus* (Hartweg) Gaines, of western North America.

The texture of our specimen was obviously thick and coriaceous, as indicated by the obscurely defined secondary and tertiary nervation; and the symmetry of shape, as well as the presence of a petiole, would seem to indicate that it was a terminal rather than a lateral leaflet, which latter are prevailingly unsymmetrical and sessile in existing species.

Several fossil species have been described from Tertiary deposits of the western United States, among which may be mentioned *Odostemon simplex* (Newberry) Cockerell (= *Berberis simplex* Newberry³) as an example of their general foliar type; but, from the figures, it may be seen that none is likely to be confused with ours.

³ Newberry, J. S. U. S. Geol. Survey, Mon. vol. 35 (The later extinct floras of North America), p. 97. pl. 56, fig. 2. 1898.

The specific designation, *Reynoldsii*, is given in recognition of Mr. Edmund Reynolds, the collector of the specimen.

Staphylea Viridifluminis n. sp. Capsule, flattened, ellipsoidal or obscurely obovate in outline, 4.5 cm. in length by 2.75 cm. in maximum width, pedicellate, membranous and reticulate-veined throughout, apparently 3-celled or -divided, each division rounded proximad and distad, terminating distally in a short awn or bristle, the three divisions compacted proximad, forming a curved-cuneate, apiculate base; sepals inferior, obscurely defined; pedicel about 3 mm. in length. Mus. New York Bot. Gard. No. $\frac{5.8}{1}$ (plate 2, fig. 3).⁵

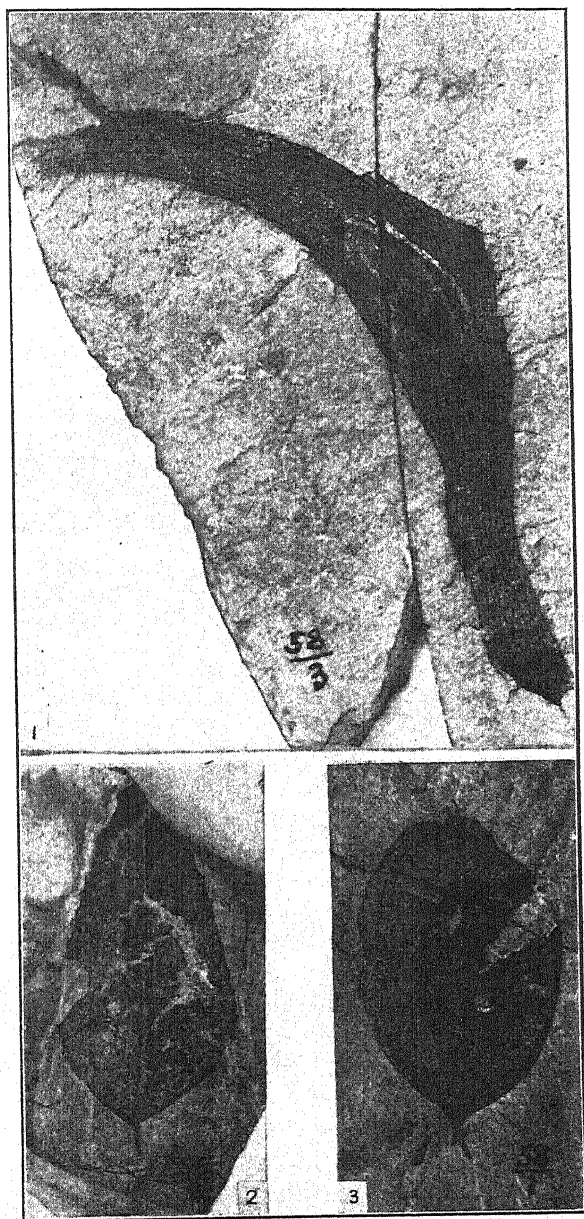
This specimen obviously represents a compressed and ruptured pod or capsule belonging to the genus *Staphylea*, and one so closely comparable with those of the existing *S. trifoliata* Linnaeus as to be impossible of differentiation if, for example, a flattened herbarium specimen is utilized for comparison. Incidentally, also, attention may be called to the rounded and the longitudinal markings in the median part of our specimen, which are strikingly suggestive of impressions of seeds and their accompanying placentae.

Several American Tertiary species of *Staphylea*—based upon the leaflets only—have been described and figured. One of these in particular—*Staphylea acuminata* Lesquereux⁴—from accredited Miocene or Oligocene deposits in Colorado, is satisfactorily identifiable with the genus; and, in as much as its geologic age is relatively close to that of our specimen, it might be of interest to speculate upon the possibility that these leaflets and the capsule now under consideration may be identical specifically, as well as generically. Future collections, in one or another of the deposits in which either the capsule or the leaflets were found, ought to bring such remains to light, associated together.

In conclusion the following quotation from Lesquereux' discussion (*op. cit.*, p. 267) may be of interest: 'The species [*Staphylea acuminata*] is remarkably similar, considering the leaves at least, to the North American *S. trifoliata* Linn.'

⁴ Lesquereux, Leo. U. S. Geol. Survey Terr., Rept. vol. 7 (The Tertiary flora), p. 267. *pl.* 48, *figs.* 4, 5. 1878; *idem*, vol. 8 (The Cretaceous and Tertiary floras), p. 183. *pl.* 36, *figs.* 1-4. 1883.

⁵ Plate 2 from photographs by Henry C. Hartmann.



1. PONTEDERITES THECOIDES
2. ODOSTEMON REYNOLDSII
3. STAPHYLEA VIRIDIFLUMINIS

Studies on the flora of northern South America—XII¹

H. A. GLEASON

Cyphostyleae—A NEW TRIBE OF MELASTOMATACEAE

Stems woody. Leaves 5-ply-nerved. Inflorescence racemose, terminal or axillary. Flowers 5-merous. Hypanthium and calyx densely hirsute, the calyx calyptriform, deciduous at anthesis, entire or separable into five sepals. Petals ample. Torus expanded horizontally even before anthesis, thick and fleshy, bearing the stamens and petals on its distal face, more or less arched over the mouth of the hypanthium. Stamens 5, episepalous in position, the stout filaments strongly incurved at the summit and again recurved to the erect anther; anthers oblong, stout, 2-celled, opening by a lateral pore at the summit of the deep ventral furrow; connective neither prolonged nor appendaged, continued without obvious articulation into the filament. Ovary wholly inferior, 5-celled; ovules numerous, minute, on an elongate placenta which is attached to the axial angle of the loculus by its center only. Style clavate, stout, the summit sharply curved or recurved to the broad truncate stigma. Fruit a capsule, dehiscent by 5 valves. Seeds numerous, straight, the raphe surrounded by a broad fimbriate wing.

The tribe differs from all other melastomes in numerous characters. Calyptriform deciduous calyces are rare in the family, but occur in several genera. An expanded, terminal, pentagonal, fleshy torus is unknown to me elsewhere in the family. Several genera with strongly dimorphic stamens tend to suppress completely the inner circle, as *Monochaetum*, but the condition is comparatively rare, while the shape of the stamens, with their stout anthers set on S-shape filaments, is peculiar to the new tribe. Several genera present anthers with apparently lateral pores, caused by the bending of the anther immediately at the summit, but in the Cyphostyleae the anther is straight and the pore distinctly lateral. In various genera the style is gently curved or more or less sigmoid, but no others have such an abrupt hook at the summit of a clavate style. In no other genera known to me are the placentae attached by their centers only, with their ends extending down and up through the loculus. While capsular fruits are characteristic of eight tribes of the subfamily Melastomeae,

¹ Contributions from The New York Botanical Garden, No. 307.

they proceed almost invariably from ovaries wholly or nearly superior, while here the ovary is completely inferior. Two genera are included:

Inflorescence axillary; calyx separating into distinct sepals before falling; torus sharply pentagonal, the projecting lobes simulating calyx-lobes but opposite the petals; summit of the anther arched over the pore, which is directed basally; summit of the style recurved; leaves strongly anisophyllous. *Allomaieta*.

Inflorescence terminal; calyx not separating into distinct sepals; torus round or obtusely pentagonal; summit of the anther not arched over the pore, which is distinctly lateral; summit of the style bent at right angles; leaves of each pair essentially equal in size. *Cyphostyla*.

Allomaieta gen. nov.

Characters of the tribe. Stem, leaves, and inflorescence hirsute. Leaves unequal in each pair, the smaller cordate, the larger obovate; petioles short. Inflorescence small, axillary, the branches and short-pedicelled flowers subtended by subulate bracts. Hypanthium campanulate, terminating in the acutely pentagonal torus. Sepals large, erect and connivent before anthesis, soon deciduous. Petals large, obovate, obtuse. Ovary glabrous. Stigma truncate-retuse. Fruit capsular, the hypanthium dehiscent to the middle in five valves. Seeds minute, semiovoid, the raphe surrounded by a broad, deeply fimbriate wing.

Allomaieta grandiflora n. sp. Petioles 5 or 10 mm. long, hirsute like the stem; smaller leaf-blades cordate-ovate, reflexed, 15-30 mm. long, 12-20 mm. wide, obscurely 5-nerved, abruptly acute; larger leaf-blades obovate-oblong, the largest 18 cm. long and 7 cm. wide, acuminate, entire, narrowed from above the middle to a cordate base, the auricles overlapping above the petiole, 5-plexi-nerved, the intermediate pair arising 2-3 cm. above the base; midvein densely hirsute above, secondaries prominulous only beneath, ascending at almost right angles, veinlets plane and finely reticulate; inflorescence 5-6-flowered, 2-3 cm. long; bracts 3-4 mm. long; pedicels about 2 mm. long; hypanthium 3 mm. long, obscurely 10-ribbed, densely hirsute; sepals narrowly triangular-lanceolate, 9 mm. long, acuminate, long-hirsute; petals broadly cuneate-obovate, obtuse, glabrous, entire, 22 mm. long; filaments stout, somewhat flattened, erect, about 4.5 mm. long; anthers acute, nearly 2 mm. long; ovary radially 5-ribbed at the summit; style about 5 mm. long; stigma 0.8 mm. in diameter; fruiting hypanthium about 5 mm. long, the valves spreading or somewhat recurved; seeds with semi-ovoid, sharply tuberculate body 0.25-0.4 mm. long, the wing as wide as the seed or somewhat wider.

Type, *Ariste-Joseph 1083*, collected at Paima, Dept. Cundimarca, Colombia, and deposited in the United States National Herbarium as number 1,189,081 (duplicate in the herbarium of the New York Botanical Garden).

The anthers are stout and plump, like those of *Miconia* section *Amblyarrhena*, but differ in their method of dehiscence. Toward the base of the anther, the two pollen-sacs are separated by the usual suture; in the terminal quarter of the anther the sacs are confluent and project ventrally, so that the single pore is hidden beneath this projection and is directed basally. The fruiting hypanthium is only slightly enlarged and at maturity splits from the summit backwards about halfway to the base, along the lines of the sepalar mid-veins. The summit of the capsule of course splits radially at the same time and the dissepiments break from the axis, persisting along the wall of the hypanthium and leaving a free central axis. The minute seeds are semi-ovoid in shape and somewhat pointed. Along the straight side, or raphe, the seed bears a broad, thin, deeply fimbriate membrane surrounding the raphe and large enough to double the size of the seed proper.

Cyphostyla gen. nov.

Characters of the tribe. Inflorescence densely hirsute. Leaves essentially equal, ovate-oblong, on conspicuous petioles. Inflorescence terminal, loosely flowered, with long pedicels, the bracts none or early deciduous. Hypanthium obconic, densely hirsute with reflexed hairs. Sepals erect and united into a conic calyptra, deciduous at anthesis. Petals large purple, triangularly obovate or somewhat retuse. Ovary glabrous. Stigma truncate-retuse.

Leaves ovate-oblong, sharply acuminate..... *C. hirsuta*.
Leaves oblong, subacuminate to a blunt tip..... *C. villosa*.

Cyphostyla hirsuta n. sp. Stem, petioles, and inflorescence hirsute with purplish hairs 1–1.5 mm. long; petioles 5–10 mm. long; leaf-blades firm, ovate-oblong, the largest 9 by 3.5 cm., sharply acuminate, entire, appressed-ciliate with stout hairs, rounded at the base, 5-plex-nerved, the secondaries about 2 mm. apart; upper surface pubescent on the veins with short yellowish hairs 0.2 mm. long, hirsute on the surface proper with purplish hairs 1.5–1.7 mm. long; lower surface pale green and softly villous on surface and veinlets with erect whitish hairs 0.5–0.8 mm. long, sparsely hirsute on the primaries with purplish

hairs 1–1.5 mm. long; inflorescence 1–3 cm. long, few-flowered; hypanthium 6 mm. long, 6 mm. in diameter at the summit, fleshy, completely covered with stout, simple, retrorse bristles 3.5 mm. long; calyptra 8 mm. long, hirsute like the hypanthium; petals purple, 2 cm. long and broad; filaments about 5 mm. long; anthers 5 mm. long; style about 9 mm. long.

Type, *Pennell 10,963*, collected at Primavera, Dept. Antioquia, Colombia, alt. 1800–2200 m., 22 Sep. 1922, and deposited in the herbarium of the New York Botanical Garden.

Cyphostyla villosa n. sp. Stem, petioles, and inflorescence pubescent, more densely toward the summit, with brownish papillose hairs 1–1.2 mm. long, the terminal seta soon deciduous; petioles 10–25 mm. long; leaf-blades oblong, thin, the largest 13 by 5 cm., subacuminate to a blunt tip, entire, obtuse at base, 5-plexi-nerved, the secondaries 3 mm. apart; upper surface scabrous with short conic projections, many of which are tipped with strigose yellow hairs 1–1.5 mm. long, and villous on the veins; lower surface thinly villous on surface and veins alike with whitish hairs 0.5–1 mm. long; inflorescence 10–15 cm. long, the lower pedicels as much as 3 cm. long and all jointed 5 mm. below the summit; hypanthium 5 mm. long, densely hirsute with reflexed hairs 3 mm. long; calyptra 15 mm. long, hirsute like the hypanthium; petals purple, triangular, slightly retuse, 25 mm. long and broad; filaments 5 mm. long; anthers 3.5 mm. long; style 7 mm. long.

Type, *Toro 1038*, collected at Fredonia, vicinity of Medellin, Dept. Antioquia, Colombia, 30 June 1928, and deposited in the herbarium of the New York Botanical Garden. The mature fruit and seeds of both species *Cyphostyla* are as yet unknown.

HYPERICUM, SUBSECTION EUBRATHYS, IN NORTHWESTERN SOUTH AMERICA

The genus *Hypericum* is represented in northern South America only by the section *Brathys*. Of the numerous species in the region, the most striking in appearance are the shrubs of the subsection *Eubrathys*, characterized by their freely branching, usually bushy habit and their small, crowded, frequently imbricate leaves. Considerable confusion has developed in the identification of the material of this subsection in American herbaria, due primarily to the lack of any adequate monographic treatment since 1862, when Triana and Planchon dis-

cussed the species of Colombia. Keller supplied a key to the species of the group in 1908, unaccompanied by descriptions and citations, except for a few new forms therein proposed, and almost the same arrangement reappeared in the second edition of the *Natürlichen Pflanzenfamilien*. As a further contribution to our knowledge of the group, the following key is offered, based primarily on the large amount of material in the herbarium of the New York Botanical Garden, which has been compared with the equally copious material at Kew and Berlin. It has been possible to see either types or authentic material of nearly every published species.

All members of the group agree in the general structure of the flower, exhibiting lanceolate to ovate or obovate, rather stiff and erect, green sepals, strongly inequilateral, oblong to obovate-rotund, yellow petals, numerous (12-120 or more) distinct stamens, and three (rarely four or five) styles, which are connate only in the single species *H. aciculare* HBK., of Ecuador. I have not dissected this species and it is omitted in the key. Differences in the shape of the petals exist among the species, but their shape can not often be ascertained with accuracy, even after careful dissection. Diagnostic characters lie chiefly in the number of stamens and in the dimensions and relative proportions of the different floral parts. In these features each species shows a high degree of constancy. The floral structures must always be supplemented by the foliar characters, and the leaves vary from narrowly linear to broadly ovate or obovate, from thin to stoutly ellipsoid, and from involute to flat or revolute. In the key below, the shape and size of the leaf and the size of the petals, number of stamens, and proportions of styles and ovary is given for each species. A variation of about a fifth in dimensions may be expected in any series of specimens, so that a species stated to have petals 10 mm. long will probably show extremes of 8 and 12 mm.

Group 1. Leaves only 2-6 mm. long.

Petals more than 10 mm. long; stamens about 100; styles 5-8 mm. long and 2-3 times as long as the ovary.

Leaves flat.

Leaves recurved-spreading, crisped on the margin when dry, averaging 2-3 mm. long.....*H. thuyoides* HBK.

Leaves strictly erect, thick, firm, or subfleshy.

- Leaves rather remote, ovate, flat, averaging 4 mm. long
 *H. Hartwegi* Benth.
- Leaves imbricate, narrowly ovate, involute or boat-shaped, those
 of the flowering branches only about 2 mm. long
 *H. myricariifolium* Hieron.
- Leaves linear, involute. *H. laricifolium* Juss.
- Petals 5-9 mm. long; stamens few or many; styles 1.5-4.5 mm. long.
- Leaves thick and fleshy, somewhat boat-shaped, linear to oblanceolate,
 erect, longer than the internodes, 1.5-2.5 mm. long; stamens about 60;
 styles twice as long as the ovary. *H. Lindenii* Keller.
- Leaves linear, involute, acerose.
 Stamens about 35; styles 1.5 mm. long, twice as long as the ovary
 *H. bryoides* Gleason.
- Stamens about 90; styles 4.3 mm. long; ovary 3.5 mm. long
 *H. laricoides* Gleason.
- Leaves flat, strictly erect and imbricate, somewhat fleshy or firm, ovate,
 about 5 by 3 mm.; stamens about 45; styles about 3 mm. long, twice
 as long as the ovary. *H. quitense* Keller.
- Leaves flat, thin, spreading, conspicuously exposing the quadrangular
 internodes, mostly 3-6 mm. long.
 Stamens 20-30; styles 2mm., ovary 1.4 mm. long
 *H. loxense* Benth.
- Stamens about 100; styles 4.5 mm., ovary 1.5 mm. long
 *H. carinosum* Keller.

Group 2. Leaves revolute.

- Stamens about 100; petals 13 mm. long; styles 8 mm. long, three times as
 long as the ovary; leaves linear, 8-10 mm. long
 *H. chamaemyrtus* Tr. & Pl.
- Stamens about 25; petals 8-10 mm. long; styles 0.5 mm. long, less than half
 as long as the ovary; leaves lanceolate, 1 cm. long
 *H. gnidioides* Seemann.

Group 3. Leaves narrowly linear, acerose, involute, about 10 mm. long.

- Stamens 12-40; petals 4-7 mm. long.
 Styles normally 5, about equaling the ovary. *H. Brathys* Lam.
- Styles 3, much shorter than the ovary. *H. strictum* HBK.
- Stamens 60-120; styles about equaling the ovary.
 Petals about 7mm., filaments 4 mm., styles 1.9 mm. long
 *H. Holtoni* Gleason.
- Petals 10-14 mm., filaments 6 mm., styles 4-4.5 mm. long.
 Leaves acicular, about 1mm. wide, closely involute
 *H. struthiolaefolium* Juss.
- Leaves linear, 2-4 mm. wide, scarcely involute
 *H. Weberbaueri* Keller.

Group 4. Leaves flat, 6-25 mm. long.

- Stenophyllous species: leaves 2.5-4 mm. wide and 4-8 times as long.

Styles 1.5–2 mm. long, about half as long as the ovary.

Stamens 20–30; styles 4; petals about 5 mm. long

..... *H. Jahonii* Keller.

Stamens about 50; styles 3; petals about 10 mm. long

..... *H. lancifolium* Gleason.

Styles a third to a half longer than the ovary.

Petals 7 mm., sepals 6 mm. long; stamens 40–50.

Flowers solitary at the tips of the branches

..... *H. thymifolium* HBK.

Flowers in small clusters..... *H. Jussiae* Pl. & Lind.

Petals about 10 mm. long; sepals 9 mm. long; stamens 60–70

..... *H. Weberbaueri* Keller.

Styles 2.5–3 times as long as the ovary; stamens 80–100.

Petals 6–7 mm. long; styles 4.5 mm. long... *H. carinosum* Keller.

Petals 14 mm. long; styles 8.5 mm. long... *H. Phellos* Gleason.

Platyphyllous species: leaves 3–10 mm. wide and 2–3 times as long, or even proportionately broader; petals 10–14 mm. long.

Styles 2–3 times as long as the ovary; stamens 80–120.

Leaves elliptic, sharply acute..... *H. stenopetalum* Turcz.

Leaves obovate, obtuse or rounded..... *H. platyphyllum* Gleason.

Styles equalling or somewhat longer than the ovary; stamens 40–55.

Leaves obtuse or rounded, elliptic..... *H. mexicanum* L.

Leaves sharply acute.

Leaves ovate-lanceolate, falcate, glaucous, flabellately nerved

..... *H. pimelioides* Pl. & Lind.

Leaves elliptic, straight, green, 1-nerved. *H. caracasenum* Willd.

***Hypericum bryoides* n. sp.** Stems freely and cespitosely branched, forming compact bushes about 1 dm. high; terminal branches 1–3 cm. long, erect, densely leafy, with internodes 0.5 mm. long; leaves crowded, imbricate and beautifully decussate, ascending, sessile, lance-subulate, rather thin, involute or boat-shaped, channeled on the lower side along the midvein, conspicuously punctate in two longitudinal rows, 2.5–3 mm. long, 0.5 mm. wide before unrolling; flowers solitary on very short pedicels at the summit of the branches; sepals ovate-lanceolate, 3–3.5 mm. long, 0.9–1.1 mm. wide, obscurely 3-nerved; petals obliquely obovate, 3.5–4 mm. long, 2–2.2 mm. wide, not apiculate; stamens about 36, very irregular in length, the longest 3 mm.; ovary ovoid, 0.8 mm. long; styles 3, stout, erect, 1.5 mm. long.

Type, *Killip & Smith 19,533*, collected on the western slope of the Páramo de Santurbán, Dept. Santander, Colombia, alt. 3000 m., 18 Feb. 1927, and deposited in the herbarium of the New York Botanical Garden; also *Killip & Smith 18,631*, from Páramo de Romeral, Dept. Norte de Santander, alt. 3800–4200 m.

Hypericum loricoides n. sp. Freely branched; stems naked below with exfoliating bark; internodes 3–4 mm. long on the principal branches, their leaves linear or linear-lanceolate, acerose, involute, 5–6 mm. long; microphyllous axillary shoots freely developed, rarely exceeding the subtending leaves and bearing imbricate leaves 3–4 mm. long; flowers solitary, terminating elongated microphyllous shoots, the pedicels 1–2 mm. long; sepals ovate-lanceolate, acuminate, 6 mm. long, faintly 5-nerved; petals obliquely obovate, 9 mm. long; stamens about 90, all separate, 4.5 mm. long; ovary ovoid, 3.5 mm. long; styles 3, separate, 4.3 mm. long.

Type, *Pittier 12,713*, collected on the Páramos de Timote, Merida, Venezuela, alt. 3800–4200 m., where it forms extensive colonies, 24 Jan. 1928, and deposited in the United States National Herbarium. The plant has the aspect of *H. laricifolium*, but differs in its acerose leaves, somewhat smaller flowers, and much shorter styles.

HYPERICUM STRICTUM HBK. The species is common and widely variable. In its typical form it does not extend north of Bogota, but varieties occur in Santander and Norte de Santander.

Hypericum strictum compactum (Tr. & Pl.) new comb. (*H. struthiolaefolium compactum* Tr. & Pl.). Low caespitose shrub 1–3 dm. high; stems more or less crooked, spreading, freely and compactly branched, the branches short.

Páramos de Santurbán and Romeral, Santander and Norte de Santander. Although differing remarkably from the species in its general appearance, the flowers maintain the typical structure precisely.

Hypericum strictum reductum n. var. Floral parts all much smaller than the type, the petals 4 mm., sepals 2.7 mm., stamens about 15, the longest only 3 mm., ovary 2.1 mm., styles 1.6 mm.

Type, *Killip & Smith 19,534*, collected on the western slope of the Páramo de Santurban, toward Tona, Santander, Colombia, alt. 3000 m., 18 Feb. 1927, and deposited in the herbarium of the New York Botanical Garden.

Hypericum Holtoni n. sp. Stems freely and compactly branched, obscurely quadrangular, the principal internodes 5–7 mm. long; leaf-bearing branches rather crowded, the in-

ternodes 2–3 mm. long; leaves recurved-ascending, narrowly linear, 10–12 mm. long, involute, pungently pointed; flowers solitary, terminating the numerous short lateral branches; sepals lanceolate, acuminate, 5.5 mm. long; petals oblong, 7 mm. long, 2.4 mm. wide; stamens about 65, 3.7–4.3 mm. long; ovary 2.4 mm. long; styles 4(!), 1.9 mm. long.

Type, *Holton* 787, collected 'in montibus juxta Bogotam', Colombia, 10 Nov. 1852, and deposited in the herbarium of Columbia University at the New York Botanical Garden. With the general habit and appearance of *H. Brathys* Lam., its flower-parts are regularly larger and the stamens more numerous. It also resembles *H. strictum compactum* in appearance, but differs in the size of the flowers and number of stamens.

HYPERICUM STRUTHIOLAEFOLIUM Juss. Material has been seen only from Ecuador and farther south; numerous Colombian specimens referred here are mostly *H. strictum* HBK. or *H. Brathys* Lam.

Hypericum lancifolium n. sp. Suffrutescent, the older stems invested with minute leaf-bases, the internodes 2–4 mm. long; leaves ascending, sessile, somewhat appressed at base, narrowly linear, 10–12 mm. long, 1.5–2 mm. wide, sharply acuminate; flowers few, solitary at the end of the branches, on pedicels 2–4 mm. long; sepals lanceolate, 1.8–2 mm. wide, 8.5 mm. long; petals narrowly obovate, about 10 mm. long; stamens about 50, 4.3 mm. long; styles 3, 2 mm. long, about half as long as the ovary.

Type, *Killip & Smith* 17,138, collected on open bank, vicinity of La Baja, Dept. Santander, Colombia, alt. 2200–2600 m., 14–28 Jan. 1927, and deposited in the herbarium of the New York Botanical Garden. It is nearly related to *H. Jahnii* Keller, and differs in its three styles, larger petals, and more numerous stamens.

HYPERICUM WEBERBAUERI Keller. Weberbauer's original collection is from Peru. *Pennell* 4783, from Bolivar, Colombia, agrees with the type in all except a few trifling matters of dimensions. I also refer here *Killip & Smith* 18,187 and 18,205, from Páramo de las Puertas, Santander, in which the flowers are somewhat larger than in the type and the persistent leaf-bases are much more conspicuous.

Hypericum Phellos n. sp. Shrub 3–4 mm. high, freely branched above, the bark of the leafless branches conspicuously exfoliating, principal internodes about 1 cm. long, the upper ones 4-angled and marked with 4 rows of conspicuous rounded corky protuberances; microphyllous axillary shoots freely developed and often flowering; principal leaves widely spreading, bright green, sessile, oblong-ob lanceolate, 10 mm. long, 3 mm. wide, acute, cuneate to the base, flat, sparsely and inconspicuously punctate, 1-nerved, with a few faint lateral nerves visible on the lower side; flowers solitary, terminal, on pedicels about 3 mm. long; sepals ovate-lanceolate, 6 mm. long, longitudinally veined; petals obliquely obovate, about 13 mm. long; stamens about 100, 5–6 mm. long; ovary ovoid, 3.5 mm. long; styles 3, separate, 8.5 mm. long.

Type, *Killip & Smith 18,199*, collected on Páramo de las Puentes, above La Baja, Dept. Santander, Colombia, alt. 3700–3800 m., 25 Jan. 1927, and deposited in the herbarium of the New York Botanical Garden. Other specimens by the same collectors are *15,650* and *17,727*. *H. Phellos* has a general similarity to *H. Jussiaei* Pl. & Lind. and *H. thymifolium* HBK., but is distinguished by its larger petals, longer styles, and more numerous stamens, as well as by the remarkable development of cork along the younger internodes. These protuberances become flattened out on the older twigs and finally exfoliate and disappear.

Hypericum platyphyllum n. sp. Stems woody, stout and crooked, 5–15 dm. high, freely branched above, leafy only on the smaller branches, the leaves often persisting below as appressed scales; principal internodes only 1 mm. long; leaves decussate, spreading at an angle of about 60°, densely imbricate, coriaceous, pale-green, oblong-obovate, 6 mm. long, 3 mm. wide, obtuse or rounded, cuneate to the base, the upper surface freely, the lower sparsely punctate, a few irregular lateral veins visible on the lower side; flowers solitary, terminal, nearly sessile; sepals oblong-obovate, 5.7–7 mm. long, 2–2.4 mm. wide, inconspicuously longitudinally nerved; petals obliquely obovate, about 14 mm. long; stamens 80 or more, about 7.5 mm. long; ovary ovoid, 2.5 mm. long; styles 3, separate, divergent, 5 mm. long.

Type, *Killip & Smith 18,626*, collected on the Páramo de Romeral, Norte de Santander, alt. 3800–4200 m., 30 Jan. 1927, and deposited in the herbarium of the New York Botanical Garden. Other specimens agreeing with the type are

Killip & Smith 18,559 from the same páramo and *17,496* and *17,515* from Páramo de Santurbán. Their number *15,616*, Páramo de las Vegas, has less crowded leaves 10 by 5 mm.; *18,580*, Páramo de Romeral, has narrower, subacute leaves on longer internodes, frequently with microphyllous axillary shoots, and is referred here with hesitation. *H. platyphyllum* resembles *H. mexicanum* L. in general habit, but differs in its smaller leaves, longer and more numerous stamens, proportionately longer styles, stout crooked stems, persistent leaves, and absence of persistent petiolar scars.

THE GENUS *MARIPA*

The genus was founded by Aublet in 1775, with the single species *Maripa scandens*. Earlier in the same volume he also founded the genus *Mouroucoa*, with the one species *M. violacea*. The latter is now generally recognized as a *Maripa*, and its priority of position led Kuntze to transfer to it all the later species of *Maripa*. Both of Aublet's genera are illustrated in his usual style, and these plates become of the greatest value in associating his names with current herbarium material, since the types are now practically worthless. The obvious points of difference are the large flowers, conic ovary, and long filaments in *Mouroucoa*, in contrast with the small flowers, ovoid ovary, and short filaments of *Maripa*.

The further growth of the genus is shown below.

- 1818. *M. erecta* G. F. W. Meyer, Prim. Fl. Esseq. 115. British Guiana.
- 1845. *M. glabra* Choisy, DC., Prodr. 9: 327. French Guiana.
- 1846. *M. densiflora* Benth., Hook. London Jn. Bot. 5: 351. British Guiana.
- 1869. *M. passifloroides* Benth., in Mart. Fl. Bras. 7: 207. Alto Amazonas.
M. cayennensis Meissn., op. cit. 208. French Guiana.
M. axilliflora Mart., op. cit. 208. Eastern Peru.
M. cordifolia Klotzsch, op. cit. 209. British Guiana.
- 1881. *M. nicaraguensis* Hemsl., Biol. Centr. Am. 2: 382. Central America.
M. panamensis Hemsl., l. c. Panama.
- 1891. *M. paniculata* Barb. Rodr., Vellozia ed. 2. 1: 59. Brazil.
- 1892. *M. longifolia* Sagot, in Hallier, Engl. Jahrb. 16: 525. French Guiana.
- 1920. *M. scandens argentea* Benoist, Bull. Mus. Hist. Nat. Paris 26: 560.
French Guiana.
- 1920. *M. repens* Rusby, Descr. S. Am. Pl. 103. Venezuela.
- 1922. *M. reticulata* Ducke, Arch. Jard. Bot. Rio Janeiro 3: 248. Brazil.
M. tenuis Ducke, op. cit. 249. Brazil.
- 1925. *M. scandens albicans* Ducke, op. cit. 4: 170. Brazil.

Maripa villosa Spreng., *M. spectabilis* Choisy, and *M. acuminata* Rusby are excluded from the genus.

The determination of the application of the older names to current herbarium material is a matter of some difficulty. *Mouroucoa violacea* Aubl. has very large flowers and elongate filaments: in these respects it suggests *Maripa passifloroides* Benth., as Sagot suggested on the label of his own specimen. I agree with Sagot in this belief, but do not consider it advisable to resurrect a specific name which has been in disuse for so long a time, unless on the most positive evidence. *M. scandens* Aubl. is characterized by the author as having a cinereous calyx and filaments about as long as the anthers. But one species from the Guianas presents this combination and it is quite probable that the name rightfully belongs here. But Aublet's illustrations are notoriously inaccurate and his descriptions usually omit or neglect the characters now known to be of chief taxonomic value, so that we have no positive proof of the application of his name to this or to any other species. Meissner applied the name to a plant with long filaments, common in French Guiana, and I believe we had better give his opinion the benefit of all possible doubt. *M. erecta* Meyer was based on a plant described by Rodschied as an 'arbor alta elegans,' and this statement has been accepted and continued by recent authors. There is not the slightest reason to believe that *Maripa* is ever arborescent, or that it ever fails to climb unless forced into a trailing habit by lack of proper support. I have accepted Meissner's reference of *Wulfschlaegel* 821 to this species and have accordingly considered it a synonym of *scandens*. *M. cayennensis* Meissn. appears to be the same. The types of the remaining species of northern South America have been examined.

Corolla deeply 5-fid, the lobes not connected by membranous plaits, 13.5 mm. long over all; filaments dilated at base into flat ciliate triangular appendages 1.6-1.9 mm. wide and 2.4 mm. long, the actual filament inserted on the back just below the summit of the appendage; flowers in axillary racemes; leaves cuneate at base. 1. *M. axilliflora*.

Corolla-lobes connected by membranous plaits; flowers in terminal panicles. Expanded corollas 55-65 mm. long, of which the actual tube constitutes about a fourth; filaments 19-20 mm. long, the flattened base triangular, 5-6 mm. long, 2 mm. wide, glandular-ciliate; summit of filament sparsely glandular; anthers 9-10 mm. long. 2. *M. passifloroides*.

- Expanded corollas 30-45 mm. long, of which the actual tube constitutes about a half; filaments 9-14 mm. long, the summit glabrous, the expanded basal portion pubescent or glandular throughout; ovary cylindric or conic.
- Sepals ovate to rotund, even the inner three about as wide as long, the outer two glabrous or nearly so.
- Filaments sharply incurved 1 mm. below the summit and again recurved at the base of the anther, the latter erect and connivent around the style just below the stigma; expanded base of the filaments 1.4 mm. long and densely villous
-3. *M. panamensis*.
- Filaments erect, straight or essentially so, the expanded base crisp-pubescent.
- Filaments abruptly dilated below into a flat, triangular base 5 mm. long, 1.3 mm. wide, and densely short-pubescent
-4. *M. nicaraguensis*.
- Filaments stout, subulate, 1.3-1.5 mm. in diameter at base, gradually tapering to the summit, the basal 5 mm. longitudinally grooved on the inner face and pubescent with short stout hairs.....5. *M. colombiana*.
- Sepals rotund to transversely oblong, the inner three much wider than long, the outer two densely sericeous.....6. *M. scandens*.
- Expanded corollas mostly less than 25 mm. long, of which the actual tube constitutes about half; filaments 2.5-8 mm. long; inner three sepals not more than 7 mm. wide; ovary subglobose to ovoid or short-cylindric.
- Outer two sepals densely sericeous; filaments 4-6 mm. long (or rarely a trifle longer), glandular on the triangular base; ovary short-ovoid, glabrous.....7. *M. cordifolia*.
- Outer sepals glabrous, but covered with minute shining resinous particles.
- Filaments about 4.3 mm. long, the expanded base glandular-pubescent with hairs about 0.2 mm. long; ovary short-ovoid, densely villous at the summit.....8. *M. densiflora*.
- Filaments about 8 mm. long, the expanded base densely villous with minutely glandular crooked hairs 0.5-0.8 mm. long; ovary short-cylindric, glabrous.....9. *M. repens*.
- Outer sepals glabrous; filaments 2.5 mm. long, the expanded base glandular-ciliate; ovary stoutly ellipsoid, glabrous
-10. *M. glabra*.
- Flowers unknown.....11. *M. longifolia*.

1. MARIPA MAXILLIFLORA Mart. Tarapoto, Peru: Spruce 4230 (type). The original description is adequate and is accompanied by an accurate plate.

2. MARIPA PASSIFLOROIDES Benth. (*Mouroucoa violacea* Aubl.?) Alto Amazonas: Spruce 1419 (type); British Guiana:

Hohenkerk 713; French Guiana: *Sagot* 1160. Meissner's plate in *Flora Brasiliensis* indicates a deeply 5-fid corolla, which is not in accordance with the facts. It is distinguished even in foliage by the reticulate venation on the upper leaf-surface.

3. *MARIPA PANAMENSIS* Hemsl. Panama: *Fendler* 255 (type), *Williams* 985, *Pittier* 3994, 5489. The fruit is ellipsoid, 3 cm. long, longitudinally ribbed, and sharply cuspidate.

4. *MARIPA NICARAGUENSIS* Hemsl. Nicaragua: *Tate* 245, 418 (type); Honduras: *Wilson* 633.

5. *Maripa colombiana* n. sp. Branches flexuous, the flowering stems erect, stout, irregularly angular, becoming furfureous-puberulent in the inflorescence; panicle or raceme apparently 1-2 dm. long, the lateral peduncles 2-3 cm. long, jointed in the middle, and bearing one or two flowers; outer sepals leathery, thinner at the margin, subrotund, 8 mm. long, 8.5 mm. wide, glabrous, inner sepals leathery, thinner at the margin, subrotund, 8.3 mm. long, 8.6 mm. wide; corolla 40 mm. long, the tube 22 mm. long and glabrous, the lobes lanceolate, 18 mm. long, densely sericeous with short hairs, the plaits glabrous; stamens attached 4.5 mm. above the corolla-base; filaments straight, subulate, nearly terete, 11.6 mm. long, gradually tapering to the apex, 1.3-1.5 mm. in diameter below, the basal 5 mm. longitudinally grooved on the inner face and densely pubescent with short, stout, simple, rather crooked hairs; anthers 7.5 mm. long; ovary cylindric, acuminate, 5 mm. long, 2 mm. in diameter, glabrous; style 13.5 mm. long.

Type, *André* 2355, collected near Salento, Dept. El Cauca, Colombia, 13 Mar. 1876, and deposited in the herbarium of the Royal Botanic Gardens at Kew. Mature foliage leaves are not present on the specimen.

6. *MARIPA SCANDENS* Aubl. (*M. erecta* Meyer, *M. cayennensis* Meissn.). British Guiana: *Hancock* 96, *Schomburgk* 110, *Jenman* 4874, *De La Cruz* 1372, 1538, 2837, 4483, *Persaud* 123; Surinam: *Hostmann* 1251, *Wulfschlaegel* 821; French Guiana: *Sagot* 379, *Melinon* 378 (1877), (1863), (1864).

7. *MARIPA CORDIFOLIA* Klotzsch. British Guiana: *Parker*, *Schomburgk* 1469 B. (type), *Im Thurn*, *Jenman* 20, 695, 2499, 2500, *De La Cruz* 2515, 2635, 2811, 4412, *Lang* 64.

8. *MARIPA DENSIFLORA* Benth. Alto Amazonas: *Spruce* 1928; British Guiana: *Schomburgk* 232.5 (type).

9. *MARIPA REPENS* Rusby. Venezuela: *Rusby & Squires* (type).

10. *MARIPA GLABRA* Choisy. French Guiana: *Sagot 1398*, *Melinon 141* (1854), 523 (1864), (1864).

11. *MARIPA LONGIFOLIA* Sagot. It is possible that Hallier was unaware that his recognition and brief mention of Sagot's manuscript name was valid publication of a new species. It is apparently based on *Sagot 1201*, which bears Sagot's name in his own hand, accompanied with the note 'affinis Maripae guianensi (syn. *M. scandente*) a quo foliis statim diagnoscutur.' The leaves are elongate oblong, 14–18 cm. long, 4–5.5 cm. wide, acuminate to a falcate apex, cuneate to an acute base, conspicuously veined. The fruit is pyriform, 2 cm. long, and obtuse.

A RARE UTRICULARIA FROM BRITISH GUIANA

UTRICULARIA BENJAMINIANA Oliver, Jour.

Linn. Soc. 4: 176. 1860.

Akentra inflata Benj. Linnaea 20: 319. 1847.

Utricularia puberula Klotzsch, Schomburgk, Reisen in Brit.-Guiana 3: 1159. 1848. *Nomen nudum*.

Utricularia inflata (Benj.) Pulle, Enum. Vasc. Pl. Surinam 419. 1906.

This rare species has been collected but four times, by Melinon and by Le Prieur and Sagot in French Guiana, by Hostmann (no. 85) in Surinam, and recently by La Cruz (no. 4514) in British Guiana. Benjamin mistook the large spur for the lower lip and regarded the real lower lip as the upper; this suggested the generic name *Akentra*. Oliver, examining the same collection of Hostmann rectified the error, but failed to discover the upper lip. Klotzsch's name was never properly published, but its application is shown by the appearance of this name in his hand on a sheet of Hostmann in the Berlin herbarium. Pulle's combination is of course antedated by *U. inflata* Walt. The ample material in the La Cruz collection permits the completion of the description and the provision of more exact measurements.

Lower part of the flowering branches densely tomentose, bearing a whorl of 4–7 ampullae; ampullae 1–2 cm. long, narrowly fusiform, pubescent, bearing filiform, repeatedly branched, pubescent leaves at and near their apices; peduncle glabrous, 10–15 cm. high; inflorescence many-flowered, racemose,

the internodes elongating during and after anthesis to as much as 12 mm.; bracts solitary, scarious, broadly ovate, 0.7–0.9 mm. long, acuminate, slightly saccate at the broadly sessile base; pedicels glabrous, filiform, ultimately 2.5 mm. long; sepals 2, distinct, 0.9 mm. long, the adaxial broadly obovate, the abaxial almost round; corolla divided almost to the base into two very unequal lobes; upper lip erect in bud, nearly straight, 3.2 mm. long, 2 mm. wide at base, bilobed to the middle; lobes broadly semi-ovate, 1.2 mm. wide at base, the upper margins nearly straight and connivent, obtuse; lower lip 6.7 mm. wide, 5.9 mm. long, broadly rounded, abruptly spreading above the very short contracted base, palate none, but the center of the lip somewhat elevated around the opening into spur, which is 2.7 mm. long and about 1 mm. wide; spur directed forward at an angle of about 30° from the lower lip, 10 mm. long, obtusely ellipsoid, 3.3 mm. in diameter, slightly laterally flattened, slightly bilobed at apex along the median line; filaments nearly straight, 0.7–0.8 mm. long, flat, scarious-winged; anthers nearly hemispheric, 0.5 mm. in diameter; ovary globose-ovoid.

INDEX TO AMERICAN BOTANICAL LITERATURE

1926-1928

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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• Pollen grains in the identification and classification of plants

III. The Nassauvinae

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(WITH PLATE 3)

A study of the pollen grains of the Compositae has shown that, though the family as a whole is characterized by much uniformity and closeness of relationship there exists within it a wide range of pollen-grain forms. The differences in the size, shape, texture and adornments of the grains of the different species are sometimes truly enormous; still the grains are all stamped with a 'family resemblance' which is in keeping with the various degrees of interrelationship.

Though the Compositae are the largest and most clearly defined of all the families of the flowering plants, there is much uncertainty as to the relationship of the various tribes and subtribes to each other, and of the relations of the family as a whole to other families. Nevertheless the pollen grains of the various tribes and subtribes generally possess certain characters which distinguish them readily enough from those of others; and since these characters, when compared throughout groups of the Compositae of known relationships, show more or less definite trends of genetic development, it is to be expected that their further study will throw some light upon the more obscure or doubtful relationships, and possibly by projecting backwards these known lines of development, suggest the origin of the family as a whole.

The characters of pollen grains belong in a category quite apart from that of the grosser anatomical structures, though of similar phyletic distribution. Harper (1913) has shown in his studies of *Pediastrum* that 'specifically inherited cell form and cellular interactions during growth are the principal morphogenetic factors in the development of the differentiated cell colonies,' and he has shown that the number of cells and consequently their arrangement in the colonies is, to a certain extent, a matter of individual variation and of little use in the identification or classification of the different species, but that the degree to which the spines of the individual cells develop

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affords a basis for the delimitation of species, and further (1918) the number of the spines on each of the peripheral cells of the colony affords the means of making the major divisions of the genus. The laws which Harper has established for *Pediastrum* are universal, but in the highly organized plant body of the phanerogams the specifically inherited cell forms of tissue cells are largely prevented, by their interactions with their neighbors and their subservience to their functional requirements, from coming individually to expression; so that in studying the completely organized plant body we are dealing mainly with the results of the inherited 'cellular interactions' further modified by outside environmental conditions, which is but half the story. The other half, the specifically inherited cell form is to be found in the pollen grains which are comparatively much less modified by cellular interactions and certainly bring to expression their specific capacities in a freer environment than that of the somatic cells. Consequently most of the characters of pollen grains are those of the specifically inherited cell form.

Making use of the characters of the pollen grains, which have hitherto been neglected in all phylogenetic studies of the Compositae, it is the purpose of the present series of studies to see to what extent the pollen-grain characters will substantiate or refute the current ideas of the classification of the family. The results obtained from my previous investigations of the Ambrosiaceae and of *Barnadesia* encourage me to hope that a similar study of the pollen-grain forms of all the groups of the Compositae will help to establish the interrelationships of the various tribes and the origin of the group as a whole. With this in view the present paper presents an analysis of the pollen-grain forms of one of the subtribes of the Mutisieae, the Nassauvinae.

HABIT AND DISTRIBUTION OF THE NASSAUVINAE

The Nassauvinae constitute rather an isolated group of Compositae, comprising some hundred and seventy-five species in fifteen genera. Their relationships with the rest of the family are somewhat uncertain; their corollas, always distinctly bilabiate, are those of the Mutisieae, but their style branches, except in *Proustia*, 'tronquées et penicellées à l'extrémité,' are those of the Senecioneae, to which group in some genera, the

involucre and general habit bear a close resemblance. Nevertheless there is no doubt in the minds of most botanists that the Nassauvinæ belong properly in or near to the Mutisieæ.

In distribution the Nassauvinæ are almost entirely confined to the western part of South America or, more especially, to the extratropical or Chilean region, which is the one region in the world where the Mutisieæ are the dominant Compositæ, comprising nearly one third of all the family. A few genera of the Nassauvinæ, however, are represented fairly abundantly in the Andean region to the north; a few reach through the mountainous regions of Central America and Mexico, and two genera are represented even in the southwestern part of the United States. Some species of *Jungia* are native of Brazil and Colombia, and one species of *Perezia* is found on the shores of Tierra del Fuego. Roughly speaking they reach from California to Cape Horn, with their greatest concentration of species and individuals in the Andean region.

Of the fifteen genera included in the Nassauvinæ the pollen from species of eleven genera has been examined. These eleven genera are described below.

Jungia Linn. f. comprises about twelve species in Chile and Brazil, a few extending as far north as Colombia. The plants of this genus have much of the habit and occasionally the involucre of the Senecioneæ, but they are mutisiaceous in their essential characters, and are regarded by Bentham and Hooker (1873) as most closely related to the next genus.

Trixis P. Browne comprises about eleven species, mostly shrubs of diverse habit but frequently resembling the Senecioneæ. A genus of wider distribution than *Jungia*, *Trixis* reaches from Chile through Central America to Mexico and the West Indies, and two species are found in the southwestern part of the United States.

Nassauvia Jus. comprises about twenty-five species of low sprawling shrubs. In some the leaves are closely appressed, giving the branches a scaly serpent-like appearance; in others they are spreading and spine-tipped. The species of this genus are confined to the Chilean Andes, Patagonia, and the Falkland Islands, with one species reported from Cape Horn (Macloskie, 1906).

Triptilion Ruiz et Pav. comprises about six species confined

to the Chilean region and Patagonia, annual and perennial herbs of various habit, but in essential characters scarcely different from *Nassauvia*.

Proustia Lag. comprises about six or seven species in the

TABLE 1
Pollen-grain characters of the Naussavinae

NO TRACE OF SPINES IN ANY SPECIES, TEXTURE ALWAYS FINELY BUT DISTINCTLY GRANULAR	SHAPE			FURROW				transverse furrow	polar elev.	SIZE IN MICRONS
	Spheroidal	ellipsoidal	flattened	tapering	rounded	flecked	marginate			
<i>Jungia pauciflora</i> Rusby	+			0	+	+	+	0	0	27.5
<i>J. floribunda</i> Less.	+			0	+	+	+	0	0	25.8
<i>Trixis involucrata</i> D. Don		+		0	+	+	0	0	+	30.0×42.5
<i>T. frutescens</i> Spreng. ^a		+		0	+	+	0	0	+	24.0×33.0
<i>T. corymbosa</i> D. Don		+		0	+	+	0	+	+	30.8×43.3
<i>T. angustifolia</i> DC.		+		0	+	+	0	0	+	30.0×40.0
<i>T. radialis</i> (L.) O. K. ^a		+		0	+	+	0	+	+	25.3×37.5
<i>Proustia pungens</i> Poepp.	+			0	+	+	0	0	0	40.0
<i>P. Krugiana</i> Urban	+			0	+	+	0	+	+	26.6
<i>P. pyrifolia</i> Lag.	+			0	+	0	0	+	sl	28.6
<i>P. Vanillosma</i> Wright	+			0	+	+	0	+	+	30.0
<i>Perezia Wrightii</i> A. Gray	+			0	+	+	0	+	0	32.5
<i>Nassauvia pyramidalis</i> Meyen										
var. <i>arachnoidea</i> O. K.			sl	0	+	+	0	0	0	25.0
<i>N. pungens</i> Phil.			sl	0	+	+	0	0	0	27.0
<i>N. serpens</i> Urv.			sl	0	+	+	0	0	0	22.5
<i>Triptilion euphrasioides</i> DC.			sl	0	+	+	0	sl	0	18.5
<i>T. Benaventii</i> Remy			sl	0	+	+	0	sl	0	24.2×18.7
<i>T. cordifolium</i> Lag.			sl	0	+	+	0	sl	0	18.1×16.5
<i>T. spinosum</i> Ruiz & Pav.			sl	0	+	+	0	0	0	23.0
<i>Pamphalea bupleurifolia</i> Less.	+			+	+	0	0	sl	0	19.8
<i>P. heterophylla</i> Less.	+			+	+	0	0	sl	0	19.8
<i>Cleantes brasiliensis</i> D. Don	+			+	0	+	0	sl	sl	27.3
<i>C. hieracoides</i> Griseb.	+			+	0	sl	0	0	0	21.9
<i>C. hieracoides</i> D. Don	+			+	0	sl	0	sl	0	20.9
<i>Polyachyrus sphaerocephalus</i> D. Don	+			+	+	0	0	0	sl	27.5
<i>Leuceria tenuis</i> Less.	+			+	+	0	0	0	0	19.4
<i>L. paniculata</i> Poepp.	+			+	+	0	0	0	0	27.5
<i>L. anthemidifolia</i> O. K.	+			+	+	0	0	0	0	23.0
<i>L. purpurea</i> Hook. & Arn.	+			+	+	0	0	0	0	25.8
<i>Moscharia pinnatifida</i> Ruiz & Pav.	+			+	+	0	0	0	0	37.0

^a *Trixis frutescens* Spreng. has often been regarded as a synonym of *T. radialis* (L.) O. Kuntze, but recent study indicates that both species may be maintained, which is also indicated by the pollen-grain size.

Chilean region with a few in Mexico and one in Cuba. They are mostly erect shrubs or climbets, superficially resembling some Gochnatinae but are easily distinguished from that subtribe by their decidedly bilabiate corollas, a character nearly or

quite lacking in the Gochnatinae. Their style branches differ from those of all other Nassauvinae in their rounded tips, but conform to the subtribe in their long spreading form. The genus has a similar distribution to, and is regarded by Bentham and Hooker as most nearly related to *Perezia*.

Perezia Lag., the largest and possibly the most wide-spread genus, comprises forty-six species, mostly low coarse herbs, frequently with spine-tipped leaves resembling holly. Most of them are confined to the high cordilleras of South America, but a few are found in Mexico and even in the southwestern part of the United States, a few in Brazil, and in Patagonia as far south as Cape Horn.

Pamphalea Lag. comprises four or five species of annual herbs erect and branching, confined to the Chilean region. The flowers are white, borne in small heads on long peduncles. The corollas are distinctly bilabiate, but the lips are generally nearly entire, lacking the two teeth of the upper and the three of the lower lip, which are well developed in most other Nassauvinae.

Cleanthes D. Don comprises four or five species confined to Brazil. In some respects they are similar to *Trixis*, and are included in that genus by Bentham and Hooker, but in other respects they are quite different and are regarded as a separate genus by Don (1829), who says 'This genus, which appears to be a very natural one, is essentially distinguished from *Trixis* by the naked receptacle,' and by Grisebach (1879, p. 216) who says that the genus is distinct, unnaturally ('invita natura') joined with *Trixis*. The plants are perennial herbs with the flowers borne in many headed corymbs on slender stems bearing few scattered sessile leaves and with larger petioled leaves at the base, after the fashion of many hawkweeds. Thus in habit they stand in marked contrast to the species of *Trixis*, which are all shrubs. The flowers of *Cleanthes* also differ from those of *Trixis* in the shorter elliptical and more minutely toothed lower lip of the corolla, and in their pappus, which is persistent, while in *Trixis* it is caducous. It will be shown that the difference between these two genera is strongly expressed in the characters of their pollen grains.

Polyachyrus Lag. comprises about seven species, annual or perennial herbs, generally very woolly or glandular-hairy. The species are about equally divided in distribution between

southern Peru and the northern provinces of Chile. The genus is very distinct, but approaches, at least in outward appearance, certain species of *Leuceria*, and is regarded by Bentham and Hooker as most closely related to that genus, though Weddell (1835) following Cassini, insists that the relationship is most closely with *Nassauvia*. As we shall see, the evidence of their pollen grains is decidedly in favor of the former view.

Leuceria Lag. comprises about twenty-five species confined almost entirely to the Chilean region, annual or perennial herbs with leaves more or less downy white; of various habit, but sometimes resembling the Cichoriaceae.

Moscharia Ruiz et Pav. consists of but a single species in Chile, an annual herb, in outward appearance bearing some resemblance to *Leuceria*. The name *Moscharia* is well chosen from the odor of musk which the whole plant gives off. This same character also suggests the common name, Almizcillo (Ruiz et Pavon, 1797, p. 91).

The characters of the pollen grains of thirty-two species of these eleven genera are displayed in table 1. It is seen that the grains of all species within each of the different genera, except for some variation in size, are essentially alike.

The distribution of the characters among the different genera is summarized in the following key. The grouping of the genera on the basis of these characters, brought out by the arrangement of the key, concurs with the classification of Bentham and Hooker; therefore it may be regarded as natural, and shows that the pollen-grain characters of these plants are correlated with the other anatomical characters.

KEY TO THE DISTRIBUTION OF THE POLLEN-GRAIN CHARACTERS

Grains entirely psilate, no trace of spines found in any species; furrows always sharply defined and extremely long, almost meeting at the poles, more or less rounded at the ends or sharply pointed (in *Cleanthes*); texture finely but conspicuously granular. Grains sphaeroidal, slightly flattened, or ellipsoidal, not conspicuously lobed, and always lacking intercolpar thickenings and concavities; various in size from 18.5μ to 40.0μ transverse measurement.

A. Furrows scarcely tapering, broadly rounded at the ends and flecked with more or less conspicuous granules.

Furrows marginate, grains approximately spheroidal. . . . *Jungia* (fig. 1)

Furrows emarginate

Grains ellipsoidal with prominent polar elevations. . . *Trixis* (figs. 2, 3)

Grains spheroidal with or without slight polar elevations. . . *Proustia*
Perezia

- Grains slightly flattened, without prominent polar elevations.....*Nassauvia*
Triptilion (fig. 4)
- B. Furrows tapering to a more or less rounded end, sharply pointed in *Cleanthes*, approximately spheroidal.
- Furrows more or less flecked.....*Pamphalea*
Cleanthes
- Furrows not flecked.....*Polyachyrus* (fig. 5)
Leuceria
Moscharia

POLLEN GRAINS OF THE NASSAUVINAE

The pollen grains of the Nassauvinae (figs. 1-5) are notable among the Compositae for two well marked characters, the absence of spines and the extreme development of the furrows. Not even the smallest vestige of spines has been found in any of the species examined; and the furrows are always sharply defined and extremely long. The lengthening has been carried to such an extent that they almost meet at the poles, the approaching ends of neighboring furrows being separated by only a narrow isthmus of unmodified exine, often less in width than the furrows themselves. There is considerable variation among the grains of the different species in the amount of tapering of the furrows towards their ends, but in those of all except one genus, the furrows are more or less rounded at the ends, and in many they are as broad at the ends as in the middle. These two characters, the entire absence of spines and the extremely long sharply defined and usually rounded furrows, are together quite distinctive for the pollen grains of the Nassauvinae, and serve to distinguish them from all the rest of the Mutisieae or the Compositae so far examined.

In other characters the pollen grains of the Nassauvinae are also rather sharply set off from the rest of the Mutisieae. In texture all are distinctly but finely granular, showing little variation in this respect, and lack entirely the coarse pebbled appearance characteristic of the grains of most of the other Mutisieae. In size they are small, ranging from 18 to 40 microns in diameter, and nearly all are less than 30 microns, while in the other tribes of the Mutisieae the size ranges as high as 57 microns in diameter, with the majority well above 30 microns. Thus the pollen-grain characters indicate that the group is rather compact and distinct from the rest of the tribe.

The pollen-grain forms of the Nassauvinae fall into two rather well marked groups as indicated in the key: those in which the furrows taper scarcely or not at all to their broad rounded ends and have the furrow surface always conspicuously flecked (group A); and those in which the furrows taper quite distinctly to their ends, which are nevertheless generally somewhat rounded, except in some species of *Cleanthes*, and have the furrow surface smooth or only occasionally slightly flecked (group B).

The tapering of the furrows is not alone always distinctive, for in both groups are encountered borderline cases, but the presence of flecks on broad nontapering furrows is quite distinctive and serves to separate the grains of *Jungia*, *Trixis*, *Nassauvia*, *Triptilion*, *Proustia*, and *Perezia* (group A) from those of the other genera of the subtribe.

The furrow flecks present the same staining properties as the cutinized material of the outer layer of the exine, as though, at the time of formation of the furrow, small fragments of the outer layer of the exine had become detached and left distributed over the surface of the furrow.

The presence of these flecks undoubtedly bears some relation to the closing of the furrow, and is probably the outcome of the lack of efficiency in closing, arising out of the broad and rounded ends of the furrows with which they are generally associated in this group. It will readily be seen that furrows of this character in the semirigid material of the exine, cannot close tightly and must remain gaping at least at the ends. Such was actually observed to be the case in some abortive and unexpanded grains. It has been shown by Tischler (1908) and others that in sterile hybrids when pollen cells abort during sporogenesis, if the abortion takes place after the rudiments of the exine have been laid down, its development is carried to completion in every detail, even though the pollen cells remain empty. It so happens that in the pollen of many normal species a few grains are to be found that are abortive and empty, yet displaying all the external details with even greater brilliancy than do the normal grains, and these remain unexpanded during staining and embedding. A striking example of this was found in the pollen of *Trixis angustifolia*, in which many grains are abortive. In the normal expanded

grains towards the ends of the furrows the flecks are numerous and close together, but in the mid-region of the furrow they are few and scattered. The explanation of this is apparent in the unexpanded grains, for in these the edges of the furrows are seen to nearly touch in the middle, but gape considerably towards the rounded ends. Nevertheless the furrow, so contracted, is tightly and evenly packed with flecks throughout its entire length. When such a furrow expands and its sides become parallel or slightly convexed, the elastic membrane bearing the flecks is stretched and in the mid-region of the furrow where the stretching is greatest, the flecks are most widely separated, while towards the ends where the stretching is less they are but little separated.

The way in which the flecks are distributed is various in the different species, sometimes offering a good specific character. For example, in the grains of *Triptilion cordifolium* and *T. spinosum*, they cover a narrow strip extending the full length and exactly in the center of the furrow, while in *T. euphrasioides* and *T. Benaventii* they are simply scattered.

The presence or absence of the rounded flecked furrow appears to indicate quite a natural division of the subtribe, for, according to the classification of Bentham and Hooker, *Jungia*, *Trixis*, *Nassauvia*, *Triptilion*, *Proustia*, and *Perezia*, the plants possessing this character (group A), are each more closely related to the other than they are to the remaining genera of the subtribe.

The grains of *Jungia* (fig. 1) are distinctly set off from those of the other five genera of group A by the possession of a slightly overhanging fold along the margins of the furrows; they are distinctly though finely granular, with the granules appearing to coalesce at the base of the overhanging part of the margins. Marginate furrows of this character are not found elsewhere in the tribe, and together with the small size, nearly spherical form, and absence of spines they serve to distinguish the grains of *Jungia* from those of all other genera.

The grains of the six species of *Trixis* (figs. 2, 3) that were examined are all essentially alike and easily distinguished from those of the other genera by their elongate form and their possession of very pronounced polar elevations, a character which reaches its maximum development in this genus. These

grains are remarkable for their large size and elongate form (table 1); in most species they are fifty per cent or more longer than broad. The long furrows are carried without appreciable tapering well up into the polar elevations. The transverse furrow is usually well defined and conspicuous. These grains present rather a striking appearance not easily confused with those of any other genera.

The grains of all species of *Proustia* and *Perezia* that have been examined are essentially alike, distinguished from those of *Trixis* and of the two following genera by their spheroidal form, and from those of *Trixis* also by their weaker development or entire absence of polar elevations. It is interesting here to note that *Proustia* is stated by Bentham (1873) to be 'very nearly allied to *Perezia*' in the Nassauvinae, but is placed by Hoffmann (1893, p. 341) next to the Chinese *Nouelia* Franchet in the subtribe Mutisinae. A comparison of the pollen grains of *Proustia* with those of the various members of the two subtribes shows that they differ distinctly from those of the Mutisinae in the absence of spine vestiges, their surface texture and their long rounded flecked furrows. In these characters, however, they harmonize perfectly with the Nassauvinae, and are almost indistinguishable from the grains of *Perezia*. So there can be little doubt of the incorrectness of Hoffmann's view in placing *Proustia* in the Mutisinae, and the correctness of Bentham's in associating it with *Perezia* in the Nassauvinae.

The grains of all species of *Nassauvia* and *Triptilion* (fig. 4), genera which are always regarded as closely allied, are indistinguishable from each other, but are easily distinguished from those of *Trixis*, *Proustia*, and *Perezia* by their flattened form and entire absence of polar elevations.

Looking back over these six genera of our group A in the key, it is seen that according to the evidence of the pollen grains, the last four genera of the group are all rather closely related, *Proustia* and *Perezia* being distinguished from *Nassauvia* and *Triptilion* only by the slightly flattened form of the grains of the two latter. The grains of *Trixis* (figs. 2, 3), however, differ from them rather widely in general appearance. They are larger, much longer and possess more prominent polar elevations, altogether presenting an appearance strikingly different from the grains of the other four genera. These

differences, however, are only of degree, involving characters which are also present to a certain extent in the grains of the other four genera. On the other hand the grains of *Jungia*, though in general appearance more like the grains of *Proustia*, are distinguished from them by the possession of marginate furrows, a character which is not even suggested in the grains of *Proustia*, *Perezia*, *Nassauvia*, and *Triptilion*. For this reason *Jungia* is more widely separated from them in the key than is *Trixis*. Whether this view is correct or not can best be decided by seeking intermediate forms; it is quite possible that among the many species of *Trixis* that have not been examined, grains will be found that are smaller, less elongate, and with less prominent polar elevations, or that among those of *Jungia* grains will be found with emarginate furrows. However this may be, the evidence of the pollen grains so far presented indicates that the six genera of group A are more closely related to each other than they are to the following group.

The remaining genera, *Pamphalea*, *Cleanthes*, *Polyachyrus*, *Leuceria*, and *Moscharia*, group B in the key, reveal much less of their interrelationships through their pollen-grain form; their visible characters are few and mostly of a negative nature. They show their distinction from those of group A in their lack of the broad rounded flecked furrows of that group, but they show their relationship to them, i.e., their position in the Nassauvinae, in the great length and generally more or less rounded ends and the sharp definition of their furrows.

The grains of *Pamphalea* and *Cleanthes* are of interest because, although unlike those of group A, their furrows taper conspicuously, they bear unmistakable flecks on their surface—small and somewhat indistinct, it is true, but none the less homologous with those of group A. This flecked character of their furrows clearly distinguishes them from those of the other members of group B, and suggests for them an intermediate position between the two groups.

The genus *Cleanthes* D. Don is not recognized by Bentham and Hooker, its species being included with *Trixis*. The pollen grains of the three species of *Cleanthes* which have been examined are all alike, and, except for their slightly flecked furrows, conform to our group B, and are quite distinct from those of *Trixis*. They differ from them in their sharply tapering fur-

rows, the much weaker development of the flecks, their spheroidal shape, and absence of polar elevations. Though there is nothing in the characters of the different species of *Cleanthes* to show that the genus is closely related to those of our section B, I believe that the absence from their grains of some of the most prominent characters of the five species of *Trixis*, is sufficient warrant for maintaining the genus *Cleanthes* separate from *Trixis*.

The grains of *Polyachyrus* (fig. 5), *Leuceria*, and *Moscharia* are essentially alike; they are small and spheroidal, with the exine perfectly smooth, and the furrows without flecks and tapering conspicuously towards their ends, which are, nevertheless, always more or less rounded.

From a consideration of the various characters of the pollen grains of the Nassauvinae and comparison with those of the other groups of the Compositae, certain lines of development are suggested. The fact that their grains are entirely without spines might be taken to indicate primitiveness, because the primitive form of a spore is smooth. Nevertheless the basic form of the pollen grain of the Compositae is unquestionably echinate. Thus the indication from this source is that the Nassauvinae may be either primitive or advanced, in fact at either one end of the development of the Compositae or at the other. The great achievement of the Composite pollen grain was the development of spines, which are quite the most conspicuous character of the grains of the majority of the species in all the tribes except the Mutisieae. Nevertheless the spines are found to be very minute or entirely absent in several widely separated groups. The cause of this smallness or absence of spines we do not always know, but certainly in some cases it is a suppression in response to the mode of pollination. For example in the Ambrosinae which are wind pollinated, I have shown (1928a) that a complete series of forms is found, ranging from that of the fully echinate grain of *Oxytenia*—a monotypic genus—which is undoubtedly primitive for the Ambrosinae, to that of the much more advanced *Euxanthium* with grains possessing only the slightest vestiges of spines. Likewise among the Anthemideae (Wodehouse, 1926), the Artemisias and their allies, all of which are wind pollinated, are nearly or quite without spines, so that in these cases there is little doubt that

the smallness or absence of spines is a suppression in response to the anemophilous habit. On the other hand, the pollen grains of some groups of the Compositae which are not wind pollinated show a strong tendency towards a suppression of spines for no apparent reason. Among the Cynareae, the tribe which is probably most closely related to the Mutisieae, many species have grains with spines greatly reduced and even occasionally entirely absent, and in the Mutisieae all of the species which have been examined, except one, have the spines greatly reduced; nevertheless, vestiges of them can nearly always be found. In the Nassauvinae, however, no trace of them has been seen in any species. Thus it appears that the developmental tendency of the spines in the Cynareae and Mutisieae is that of suppression or reduction, culminating in their entire absence in the Nassauvinae. The only alternative possible is that the Nassauvinae represent the primitive group of the Compositae from which the others took their origin, but the ease with which the spines appear to be lost in the phylogeny of the Compositae makes it seem more likely that the pollen grains of the Nassauvinae are advanced rather than primitive.

The furrow exists in all possible forms in the different tribes of the Compositae. I have shown (1928) that in the Ambrosinae the developmental tendency is a shortening of the furrow, starting with the long pointed form of the grain of *Oxytenia*, and ending with the short rounded form of *Ambrosia* and *Xanthium*. In the genera and species of the Cynareae, both the length and definition of the furrows are various and haphazard in distribution. In the grains of *Cousinia*, for example, the furrow is long, but shallow and imperfectly defined, with the surface of the intine shading gradually into that of the furrow; in *Carduus divaricatus* the furrow is medium in length, but clearly and sharply defined; in the grains of *Centrophyllum* it is so short that it practically coincides with the germinal pore; and in the genus *Centaurea* all lengths, and variation in definition may be found. Thus in the Cynareae no definite tendency is seen; the furrows are phylogenetically unstable.

In the Mutisieae, on the other hand, there is a definite tendency towards the lengthening of the furrow; in nearly all it is long, and in the subtribe Nassauvinae the lengthening is carried to its greatest extent, for in the grains of all species of

this group we have seen that the furrows almost meet at the poles, and in those of *Trixis* they are carried even beyond into the polar elevations. Furthermore in the grains of all the Nassauvinae the furrows are sharply defined; the transition in tissue from that of the general surface to that of the furrow is abrupt and the furrow is sunken so that there is no gradual change in texture in passing from one to the other, as is frequently encountered in the grains of the neighboring subtribes. The relation of the sides of the furrow to its surface in the grains of the Nassauvinae calls to mind the lids covering the ball of the mammalian eye. This reaches its best development in the grains of *Jungia*, in which the margins of the furrow bear an undulating frill, just as the lids of the eye bear lashes. A shortcoming of the analogy is that in opening, the margins of the furrows stretch the delicate membrane crossing the surface, instead of sliding over it as the lids slide over the ball of the eye.

Summarizing, it appears that the Nassauvinae may represent the culmination of three more or less distinct developmental tendencies, viz., the reduction of spines observed all through the Cynareae and Mutisieae, culminating in the entire absence of spines throughout this group; the lengthening of the furrows seen in various stages of development in the other tribes of the Mutisieae, culminating in the grains of *Trixis*; and the definition of the furrows strongly felt in the Nassauvinae, culminating in the marginate grains of *Jungia*. On the basis of the morphology of their pollen grains, the different genera of the Nassauvinae appear to be closely related and represent the end of a phylogenetic line of the Mutisieae.

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Explanation of plate 3

All figures were drawn free-hand from studies made with a Zeiss apochromatic objective, 2 mm., Na. 1.3 and a 10 \times compensating ocular, resultant magnification 900. No constant magnification is employed in reproduction. Instead a size is adopted sufficient to show the important characters. The dimensions given are the average transverse measurements; in elongate or flattened grains, the average transverse and average axial measurements.

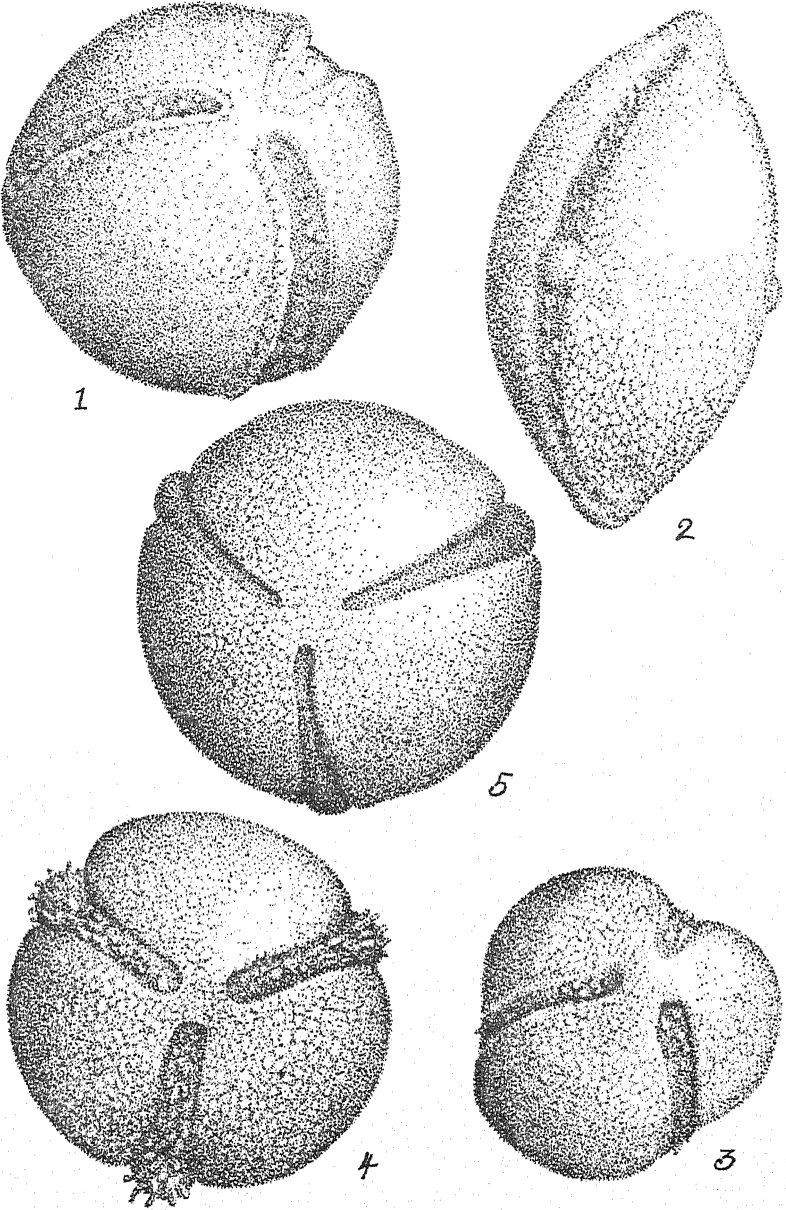
Fig. 1. Pollen grain of *Jungia floribunda* Less. 25.8 μ diam. Viewed slightly to one side of the pole, showing the long rounded flecked furrows with projecting margins.

Fig. 2. Pollen grain of *Trixis corymbosa* D. Don. 30.0 μ \times 43.3 μ . Side view showing the long rounded and flecked furrows, extending into the polar elevations.

Fig. 3. Pollen grain of *Trixis corymbosa* viewed slightly to one side of the pole, showing the closely approaching ends of the long furrows.

Fig. 4. Pollen grain of *Triptilion euphrasioides* DC. 18.5 μ diam. Polar view, showing the rounded ends of the long flecked furrows almost meeting at the pole.

Fig. 5. Pollen grain of *Polyachyrus sphaerocephalus* D. Don. 27.5 μ diam. Polar view, showing the long tapering furrows with rounded tips, but without flecks.



POLLEN GRAINS OF NASSAUVINAE

A double-walled pot for the auto-irrigation of plants¹

J. DEAN WILSON
(WITH THREE TEXT FIGURES)

In growing plants in pots for experimental or commercial purposes, it is frequently desirable to control or maintain the percentage of moisture in the soil more closely than can be done by the usual method of watering at one or two-day intervals. This can now be done very satisfactorily by the use of porous porcelain auto-irrigators (Livingston, 6, 8). By using these instruments in a number of pots with the same kind of soil, the irrigators being connected in series so that all draw water from the same reservoir and against the same resistance, it is possible to maintain the moisture content of all the pots at very nearly the same value. This may be done for long periods of time with a minimum of labor, after the necessary arrangements have been made at the start (Deatrick, 2; Dustman, 3; Livingston and Hawkins, 9; Livingston, Hemmi, and Wilson, 10). If several pots be filled with the same type of soil, each may be maintained at a different moisture content by using a mercury barostat of different height in each water system (Livingston, Hemmi, and Wilson, 10). Also, pots filled with soils of different physical characteristics and different water-holding capacities may be held at approximately the same water contents (on the basis of dry weight or dry volume) by allowing them to come into equilibrium with barostats of properly selected heights (Holmes, 5; Livingston, Hemmi, and Wilson, 10).

The auto-irrigator, as first used (Hawkins, 4; Livingston, 6; Livingston and Hawkins, 9) consisted of a cylindrical porous-porcelain cup, which was usually placed in an upright position in the mass of soil to be watered. This type was subject to difficulties, however, since the soil mass in which the irrigator was 'planted' sometimes lost its capillary contact with parts of the outer surface of the porous-porcelain wall, and successful operation requires that the porcelain-soil inter-face must be maintained, in order that the hydrostatic pressures existent in the water films of the soil mass may be quickly transferred

¹ Published with the approval of the Director of the Ohio Agricultural Experiment Station.

to those in the porous wall. A distinct improvement was introduced when the porous-porcelain cylinder was replaced by a cone of like material. When cones are used, capillary contact with the soil is maintained by gravity action, for the soil mass tends always to settle against the conical surface, and the contact between porcelain and soil should improve as time goes on.

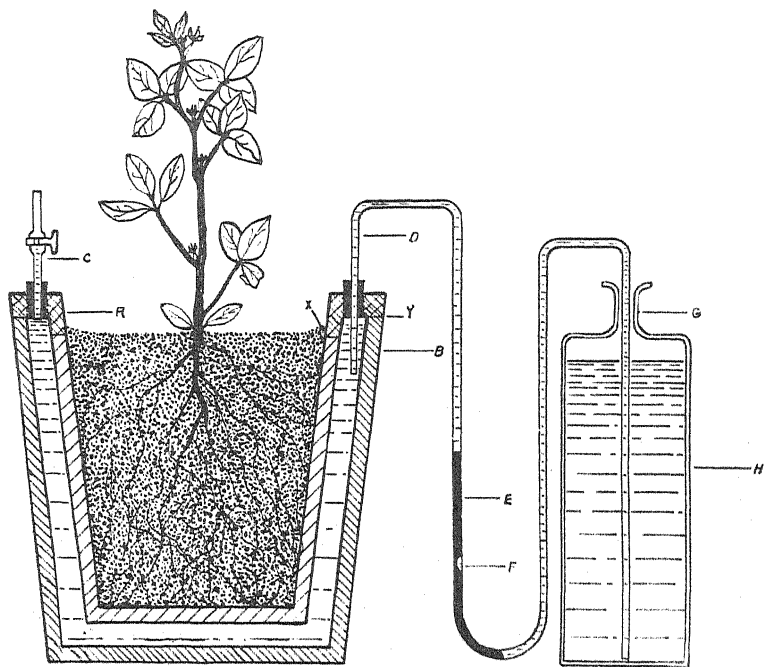


Fig. 1. Sketch showing details of a double-walled pot for the auto-irrigation of plants. This arrangement provides for the accurate determination of increments of water loss and the use of mercury barostats of widely varying heights.

Auto-irrigator cones operate best when placed centrally in the pot of soil, thus occupying the position in which it is usually desirable to place the plant. Both cone and plant cannot occupy a central position in the soil mass, but when two or more plants are placed in the same container they may be arranged around the centrally placed cone. The cone itself

occupies a considerable volume and the container consequently holds less soil when a cone is used. For these reasons it would be desirable to arrange an auto-irrigator so that the entire volume of the container would be available for soil. This has been accomplished by constructing a double-walled pot, consisting of two separate pots fastened together, either before or after firing, in such a manner that the seal is air tight. The inner pot resembles those ordinarily used for plants except that it is freely porous to water but not to air. The outer pot, which is somewhat larger than the inner one to provide for a water space between the two, is porous to neither air nor water. Arranging the pots in this way amounts simply to turning the cone type of irrigator inside out, as it were, placing the soil on the inside and the water on the outside. The result is shown, diagrammatically, in figure 1.

The inner wall, against which the soil rests and from which it draws water, consists of a porous pottery material much like that of an ordinary flower pot. The outer wall is also of pottery but it is waterproofed, the waterproofing extending over the rim and down on the inner wall to a line (*X*), the level to which the pot is to be filled with soil. This double-walled pot is made in two parts, the inner pot (*A*) having a rim or flange by which it is attached to the outer pot (*B*) at (*Y*). The two parts may be fastened together before firing or they may be kept separate in the kiln and subsequently cemented together if preferred, the process of manufacture being thus simplified. The double hatched part of the diagram represents the water-proofed portion of the inner pot.

In operation, the space between the two walls is filled with water and the inner wall is thus kept saturated. The soil rests against the slightly conical surface of the inner wall and good capillary connection is accordingly maintained by gravity. The whole cavity of this type of irrigator is available for soil and the roots of plants, and a single plant may be placed centrally in the pot. The water-supplying surface is much larger than when an irrigator cone is employed; for a 6-inch pot the porous inner wall has a surface of about 625 sq. cm., while the porous area of an irrigator cone (usually used singly in 6-inch pots of the common type or in a sheet-metal cylinder of about the same size) is only about 170 sq. cm. This larger

water-supplying surface of the new irrigator is a distinct advantage. Also, the new type may be employed in smaller sizes than could be used with the 3-inch cone irrigators. It has been tested in the 5-inch and 6-inch sizes and the pots might probably be even larger than the latter size without danger that the moisture condition of the interior of the soil mass might not be satisfactorily maintained.

The principles of operation are the same as when an irrigator cone is employed. There are two vertical, cylindrical perforations (about 18 mm. in diameter) through the rim where the inner and outer walls of the double-walled pot join, these being on opposite sides of the pot. Rubber stoppers, each bearing a tube, are inserted in these perforations. One of these tubes (*C*) is provided with a stopcock and is used for the removal of air by suction when the pot is filled with water through (*D*) at the time the irrigator is started. The tube (*D*) connects with the water reservoir (*II*). These two tubes correspond to the two tubes ordinarily attached to the cone types of irrigator by a 2-hole stopper. When the apparatus is installed suction is applied at tube (*C*), with the cock open, until air ceases to emerge. Then, the cock is closed. The hydrostatic pressure causing water movement from the reservoir to the space between the pot walls is regulated by the mercury barostat (*E*), inserted in the supply tube. As water is removed from the soil mass by evaporation from its surface or by plant absorption, it is replaced by capillary movement into the soil from the saturated porous wall of the inner part of the pot. The water content of this wall is maintained by a requisite movement of water from the reservoir. Water movement past the mercury column of the barostat is usually made evident by small bubbles, as (*F*), that rise from time to time. When movement is very slow the bubbles may not appear. A barostat of this general form has been used in earlier porous porcelain types of auto-irrigators (Livingston, 8). The height of the mercury column must be adjusted to the type of soil used; in ordinary practice it should be only 2 to 5 cm. for sandy soils, and 5 to 15 cm. for clay soils.

The increments of water loss from the outer reservoir are ascertained by refilling the bottle to a mark on its neck (*G*) from time to time, record being made of the volume of water

added in each instance, as is done in operating irrigator cones, atmometers, etc. If increments of water loss from the pot are required, the whole apparatus may be weighed at intervals, or the weighings may be made with the pot on a balance and the reservoir otherwise supported near it, the barostat tube being free to move in the neck of the bottle. Also, the barostat may be connected to a tube in the reservoir by a piece of

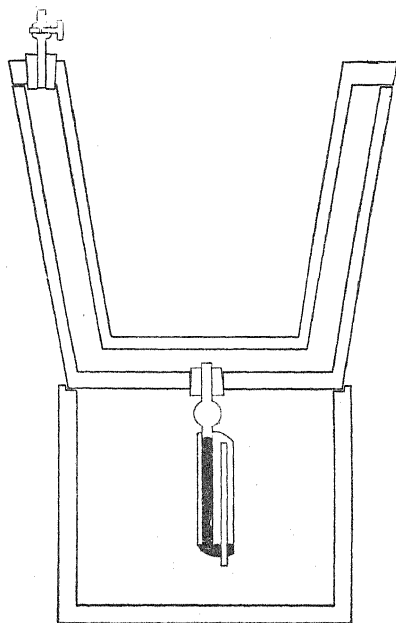


Fig. 2. A modified form of the pot shown in figure 1 in which a third pot supporting the others is used as a water reservoir. A special form of valve barostat is used here, the assembly being compact and easily movable.

flexible rubber tubing as was done in some of the experiments of Livingston and Hawkins (9). When it is desirable, the soil surface may be sealed to prevent evaporation.

The design of the irrigator shown in figure 1 was modified slightly for use in those cases where it is neither necessary to measure the amount of water used at definite intervals nor to use mercury barostats of extreme heights. This modified form is shown in figure 2.

It will be noticed that one of the holes formerly placed in the upper flange is now located in the base of the outer pot. A third pot of non-porous material serves as the outer water reservoir and also as a support for the double-walled irrigator pot. The inner reservoir is connected to the water-holding space of the lower pot by means of a specially designed barostat, as shown in the illustration. The height of the mercury column which may be used in this case is limited by the depth of the supporting pot. The ones first designed allowed for a barostat 8 cm. in height. This is sufficient to maintain all but the heavier soils at a water content low enough to be optimum for plant growth. An irrigator of this design is more compact and, in case the pots have to be moved about frequently, it eliminates the objection due to the semi-detached and somewhat unwieldy character of the outer reservoir used in the type shown in figure 1. However, it does not provide for an accurate means of measuring water losses at short intervals or for maintaining a series of pots having barostats of widely varying heights.

TESTS WITH THE IRRIGATORS

A variety of preliminary tests have been made to study the practicability of these new irrigators, and the results are given briefly in the following paragraphs.

Test 1. Two 6-inch auto-irrigator pots equipped with 5-cm. mercury columns and filled, one with muck and one with loam soil, unsealed and without plants, together with a standard, 5-cm. collodion-coated black atmometer (Livingston, 7; Livingston and Wilson, 11) placed nearby, were operated in a greenhouse for a number of weeks. Increments of water loss from each of the three reservoirs were determined at 5-day intervals and later reduced to losses in milligrams of water per square centimeter of surface area for each of the soils and the atmometer. Of course, it is understood that the spherical bulb of the atmometer and the circular, plane soil surface, the latter depressed slightly below the pot rim, were not affected alike by the environmental conditions influencing evaporation rates. The atmometer was used only to make a summation of the effect of the environmental influences affecting the evaporation rate, the results being useful in evaluating the varying losses from the two soils. The muck soil in this test consistently lost

more water per unit of surface than did the clay. Its black color gave it a greater absorptive capacity for heat than the clay possessed and its water content was somewhat higher than that of the latter, since both obtained their water past mercury columns 5-cm. in height. Each of these differences would favor a greater water loss from the muck. The atmometer lost water faster per unit of area than either of the soils. This was probably due, in part, to its very black color and thus high heat absorption, and, in part, to its more perfect exposure to conditions influencing the evaporation rate. The average for the four highest and also for the four lowest losses for 5-day intervals from each instrument are given in table 1.

TABLE 1

Losses in milligrams of water per square centimeter of exposed surface for 5-day intervals from a blackened atmometer, a muck, and a loam soil

	ATMOMETER	MUCK	LOAM
	mg.	mg.	mg.
Average of four highest values	375	312	276
Average of four lowest values	302	264	239

The losses from the three instruments for consecutive 5-day intervals paralleled each other very closely and maxima and minima occurred for the same intervals in each case. This indicates that the irrigators were able to maintain nearly constant soil moisture contents throughout the period of the test. If they have the ability to do this they should prove to be useful instruments for studying the relative rates of water loss by evaporation from the surfaces of different types of soil and through different surface mulches.

Test 2. In a comparison between irrigator losses and evaporation, measured by refilling the reservoirs to a mark on the neck each day, as was done in the preceding paragraphs, it is usually necessary to consider the lag that occurs between the time water is lost from the pot and the time it is taken up from the reservoir. To do this the pot and plant were mounted on a balance and the reservoir placed on the table beside it. A glass tube connected the pot with the water in the reservoir bottle, the tube being free to move in the neck of the bottle

without friction against the sides as the balance moved up and down. A blackened, spherical atmometer was placed on the same table near the balance. The pot was weighed and the reservoirs of the irrigator and atmometer were filled twice each day, at eight in the morning and four in the afternoon, for ten successive days. The results are shown in table 2.

TABLE 2

Mean daily water losses from irrigator pot, irrigator reservoir, and atmometer reservoir, determined at 8 a.m. and 4 p.m. each day for 10 days

PART OF APPARATUS	MEAN DAILY WATER LOSSES	
	4 P.M. TO 8 A.M.	8 A.M. TO 4 P.M.
	cc.	cc.
Reservoir	38.3	18.5
Pot	19.4	40.0
Atmometer	12.6	26.5

The lag operated in this experiment in such a way as to make the rate of water loss from the pot two to three times as great as the loss from the reservoir for a few hours in the morning (when the evaporating power of the air was increasing), while in late afternoon and night the reservoir lost water most rapidly. The pot lost water about four times as rapidly during the day period used as during the night period, while the rate of loss from the reservoir continued at a rather constant rate throughout the 24-hour period, being but little different for the day and night periods when hourly averages are computed. This would indicate a rather constant hydrostatic pressure at the pot wall at all times, regardless of the rate of loss from the soil. The pot lost water at a rate that varied in a way corresponding to the losses from the blackened atmometer as would be expected.

In this experiment, if the variation in soil moisture content were calculated on the basis of dry soil weight, the variation in the water content of the auto-irrigated soil would be about 1.2 to 2 per cent, while, if the pot were watered once each day, the variation would be 5 to 7 per cent. These variations would be greater for large plants than small ones by either method. Whether the water losses are determined by weighing or re-

filling the reservoir, they should be made at the same time each day to get comparable results. This test serves to emphasize the fact that only the mean water contents of an auto-irrigated soil are maintained and not the absolute content. It also indicates, however, that watering by this method results in a much narrower range of variation than the method of bringing the pot weight back to the same value each day. Thus, when water losses are determined by reservoir readings for 5-day intervals, as was done in some of the tests reported in this paper, the daily rates are very little modified by possible errors due to the lag between pot and reservoir. In the case of the atmometer there is no appreciable lag (it occupies, at most, but a very few minutes even under the most rapid alterations of the evaporating power of the air) and it is quite safe always to consider reservoir loss as equal, increment by increment, to the corresponding loss from the atmometer sphere itself.

Test 3. Muck soil inoculated with the organism causing club-root of cabbage (*Plasmodiophora Brassicae* Wor.) was placed in four pairs of irrigator pots, each pair with a different barostat resistance, but the two pots of each pair alike; and cabbage plants were grown in the pots from February 6 to April 24, in the greenhouse. The four barostat resistances were 2 cm., 10 cm., 20 cm., and 30 cm. of mercury. The atmometer loss was nearly uniform throughout the period of this test, being about 100 cc. for each 6-day interval.

The plants with 10-cm., 20-cm., and 30-cm. columns all grew about alike and appeared healthy throughout the period. Those drawing their water against a barostat resistance of only 2 cm. of mercury grew more rapidly at first and possessed a healthy, vigorous appearance, being of a darker blue-green color than their companion plants, whose leaves were of a more yellowish green. After about two months these most freely watered plants began to show wilting on dry days and their irrigator losses became less than before. At the end of the experiment they were found to be infected with club-root, while there was no evidence of infection in the plants grown in drier soils. The wettest soils (with mercury columns only 2 cm. high, in which infection occurred) had a water content of about 50 per cent, on the basis of dry weight, and those

with the 10 cm. columns (in which no infection appeared) had a corresponding water content of only 18 per cent. It, consequently, appears that under the conditions of this experiment the critical moisture-content limit for infection, for the muck soil used, must have been between these two water-content values. With other lengths of barostat columns, between 2 cm. and 10 cm., the limits might have been defined more precisely.

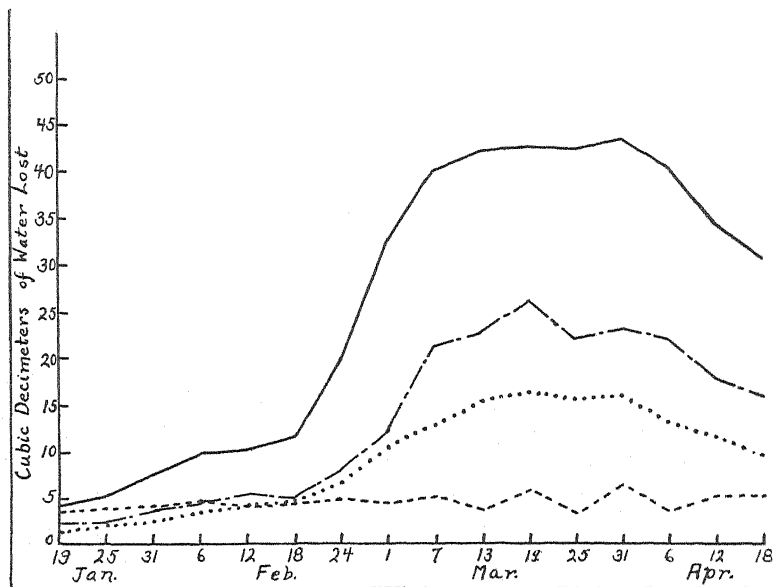


Fig. 3. Graphs showing the water losses for successive 6-day intervals from tomato plants in irrigator pots equipped with three different barostat heights and from a black, spherical atmometer. The losses corresponding to barostat heights of 5, 15 and 25 cm. are represented by the full, dot-dash, and dotted lines respectively. The atmometer losses are represented by the dash line.

This observation that cabbage is more susceptible to infection by the club-root fungus when the soil is wetter than when it is dryer than optimum, has been recorded in the literature several times (as by Chupp (1) and by Monteith (12) and others), and the result of the test here briefly described suggests that the auto-irrigator pot may be a valuable device for the study of such ecological relations.

Test 4. Three sets of 6-inch auto-irrigator pots, two in each set, all with the same loam soil, unsealed, and each with a tomato plant, but the sets with different mercury barostats, were operated in a greenhouse, together with a standard 5-cm. collodion-blackened, spherical atmometer. For one pair of pots the barostat columns were each 5 cm. high, for a second pair their height was 15 cm. and the third pair drew their water past columns of 24 cm. The increments of water loss were ascertained for 6-day intervals and each pair of corresponding values were averaged to give a single value for each interval for each pair of pots. The three resulting series of values for the pots and the single series for the blackened atmometer sphere were plotted and the four graphs thus obtained are shown in figure 3, each value being expressed in cubic decimeters.

Fluctuations in the rates of water loss, such as follow weather changes, are rather thoroughly smoothed out and obliterated by the use of the 6-day interval, and there is thus little correlation between the atmometer graph and those representing the irrigator losses. The latter all show an ascent to a maximum value and then a gradual descent. These changes were clearly not related to changes in the evaporation conditions of the greenhouse, as indicated by the atmometer graph. The steady increase in the size of the young plants and the corresponding additions to the areas of their leaf surfaces account for the ascending portions of the irrigator graphs. The exact causes for the decreasing values are less evident, but began about the time the plants flowered. Some of the lower leaves began to yellow at this time also, and the plants showed a slight drooping of the leaves on days of high evaporation. The latter fact would indicate that the pots were not supplying water at a rate equivalent to the demand set up by the large, succulent plants. It should be emphasized at this point that an irrigator of any size or type can deliver water only at a definite maximum rate corresponding mainly to the area of its porous surface and the conditions under which it is operated, such as height of mercury barostat, etc., and when a plant depending on the irrigator for its water has reached such a size that its needs are in excess of this delivery maximum, the plant will suffer from drought. Also the small mass of soil was possibly

not sufficient to supply nutrients at the necessary rate and this resulted in physiological changes within the plant which caused its water use to fall off.

The values for the 6-day increments showed pronounced and consistent differences according to the heights of the mercury column in the irrigator barostat. The ordinates of these three irrigator graphs doubtless represent approximately the transpiration rates of the corresponding plants, and also their vigor. The soil supplied with water against the lowest barostat pressure was clearly the wettest, and the plants in soils with that pressure (5 cm. of mercury) were the most vigorous and thrifty, indicating that the soil moisture content here was more nearly optimum than in those pots equipped with 15 cm. columns. The driest soil and the least vigorous plants correspond to the highest barostat pressure (25 cm. of mercury).

Test 5. A series of seven irrigator pots, filled with silt loam, were equipped with mercury barostats varying in height by 4-cm. intervals from 4 to 24 cm. The seventh pot in the series was watered with no resistance between the outer and inner reservoirs. This was done by arranging the outer reservoir so that its upper water level just corresponded with that of the bottom of the soil mass in the inner pot. Soy beans were planted in the pots and after the seedlings were well above the soil surface one good one was allowed to remain in each pot. The late fall and early winter season during which these plants were grown was found to be unfavorable to them and, consequently, the results were not all that was hoped for. However, there was a marked decrease in the rate of water use (loss from outer water reservoirs) from the wet to the dry end of the series, from 0 to 24 cm. of mercury column. A complete set of the data obtained is not given here, but in table 3 there are presented only the average daily losses for two 30-day periods (including losses from soil surface and plant leaves) for the pots equipped with barostat heights of 0, 12, and 24 cm.

The plants in the wet end of the series grew best, the one obtaining water against no mercury resistance being the largest in this test. Only one plant intermediate in the series was smaller than the one in the pot with the 24-cm. column. The reason for this break in the series was not determined. The

general appearance of the plants was also somewhat different in the wet and dry soils. The former were taller, had longer stem internodes and leaf petioles, and fewer axillary branches than the latter. The leaf number and size was much the same throughout the series, but the plants on the dry end blossomed and bore fruit more profusely than those with more available soil moisture. Some of the influences of different, maintained soil moisture contents on plant growth are shown in this test, and the irrigator pot appears to be an efficient instrument for providing such controlled moisture conditions.

Test 6. To compare the efficiency of the cone and pot types of irrigators, tomato plants were grown in soil watered by each

TABLE 3

Average daily water losses during two 30-day intervals from plants and soil in irrigator pots equipped with barostats of 0, 12 and 24 cm. in height

INTERVAL	BAROSTAT HEIGHT IN CENTIMETERS		
	0	12	24
	cc.	cc.	cc.
First	68	43	32
Second	95	67	49

instrument. Loam soil was placed in 6-inch irrigator pots and in 1-gallon tinned-metal cylinders, irrigator cones being 'planted' in the center of each of the latter. Mercury barostats 25 cm. in height were used in each arrangement. The water losses from soil and plant combined were determined at 3-day intervals over a period of two months for each type of irrigator. The results are not shown in detail, but when the average daily losses for three periods of 21 days each, covering most of the growth period of the tomato plants, were compared for each type of instrument, it was found that the losses from the pot type of irrigator were greater in every instance, but the plants watered by the cone nearly equaled the others in growth. The irrigator-pot was found to be somewhat easier to set up and operate than the cone, and may be considered an equal if not superior instrument to the latter for irrigating plants over long

periods, because of the greater area of porous surface it provides for a given soil volume.

The experiments reported in the preceding paragraphs seem to indicate clearly that this new auto-irrigator pot has promise as a research tool in physiological, ecological, agricultural, and even pathological experimentation with plants where the maintenance of a fairly constant water-supplying power of the soil is desired.

The author wishes to acknowledge his indebtedness to Professor Arthur S. Watts, of the Ceramics Department of the Ohio State University, through whose courtesy these new pots were manufactured, and to Professor B. E. Livingston, of the Johns Hopkins University, for his criticisms of the manuscript.

SUMMARY

In growing plants for experimental purposes it is frequently desirable to regulate the soil moisture content more closely than can be done by the ordinary method of adding water at one- or two-day intervals. This has been done by the use of two pots, one placed inside the other and the two fastened together by means of a flanged rim on the inner one. The inner one is porous to water but not to air, and the outer one is porous to neither. The inner pot is enough smaller than the outer to provide for a water reservoir between the two.

This pot type of irrigator permits the placing of a plant in a central position in the soil mass in which it is to be grown, and provides a much larger area of porous wall in proportion to the volume of soil to be irrigated than is the case with the older types of auto-irrigators. Otherwise, the principles of operation are similar for the various types.

Several tests to determine the usefulness and practicability of this new type of irrigator have been made. These include the following studies: one on the comparative losses of water by evaporation from different soil types and a blackened atmometer; the time lag occurring between the loss of water from a pot and its absorption from the outside reservoir; another on the possibility of maintaining such soil-moisture contents that infection of cabbage by club-root will or will not occur; a third on the variations in the amount of water used when tomato plants obtain their water past mercury barostats

of different heights, and a similar experiment for soy beans, with notes on growth characteristics of the plants; and finally, a comparison between the pot and cone types of irrigators to determine their relative efficiency as irrigators.

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Development of the integument and germination of the seed of *Eleusine indica*

MARGARET P. CUMMINS

(WITH SEVEN TEXT FIGURES)

Eleusine indica Gaertner is one of the few grasses in which the integument develops as a hard seed coat while the pericarp remains as a thin, loose layer. Because of this, a detailed study of the development and fate of the integuments has been made. Since the seeds were found not to germinate under ordinary conditions, the effect of the seed coat on imbibition was also studied.

The nature and development of the integuments has been studied in *Poa pratensis* and *Poa compressa* by Miss Andersen (1), in *Holcus halepensis* by Harrington (8), in *Zea mays*, *Triticum vulgare*, and *Avena sativa* by True (13), in barley by Brenchley (2), in *Zea mays* by Weatherwax (15) and Guignard (7), in *Poa annua* by Golinski (6), and in *Triticum vulgare* by Jensen (10). In most of these the integuments disappear or are crushed beyond recognition before maturity of the seed; but in *Poa* (1) and *Holcus* (8) at least one of the integuments persists and forms an important part of the covering of the mature seed. The writer has found in the literature no reference to the development of the integument or to germination in *Eleusine*.

Material used in this study was collected at Bloomington, Indiana, in the summer and fall of 1927. This species is abundant in this locality in alleys, gardens, and waste ground.

The ovaries containing immature seeds were imbedded in paraffin and sectioned with the microtome. The mature seeds, which were too hard to be treated in this way, were attached to blocks of wood with glue and cut freehand under the binocular microscope.

The ovary of *Eleusine* is typical of the grasses. The wall is of irregular thickness, the thicker part being at the top. It consists of an outer epidermis and four or five rows of parenchyma cells (fig. 1). The ovule is attached to the side of the ovarian cavity with the micropyle turned toward the bottom.

Just before fertilization, when the embryo-sac is mature, both integuments surround the nucellus completely. Although in most grasses the edge of the outer integument is caught in the stylar canal (Weatherwax, 15, fig. 2; Golinski, 6, pl. 2, fig. 18; Guignard, 7, p. 43-44), in *Eleusine* it continues down almost as far as the inner integument and forms only a protuberance in the canal (fig. 2).

Each integument is composed of two layers of cells except near the micropyle, where there are sometimes three layers.

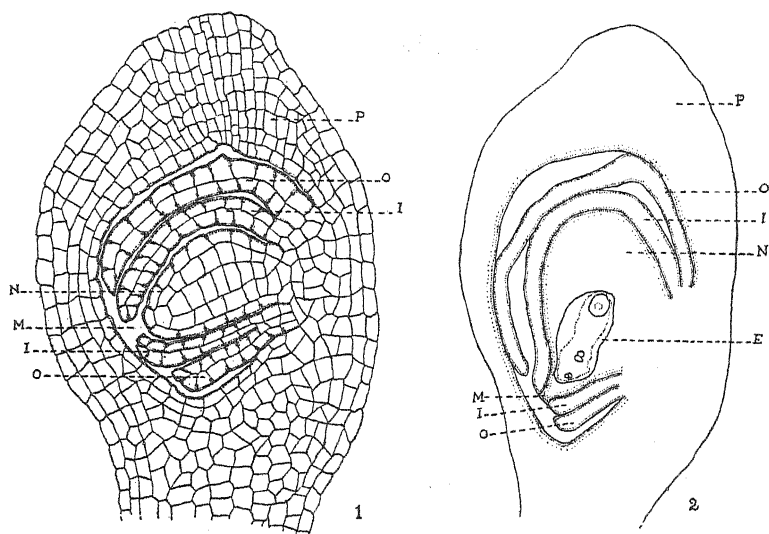


Fig. 1. Young ovary. Fig. 2. Ovary just before fertilization with both integuments surrounding the nucellus. P, pericarp; O, outer integument; I, inner integument; N, nucellar tissue; M, micropyle; E, embryo sac.

Long before fertilization the cells of the inner row of the inner integument are larger and stain more densely than the others (fig. 3). A radial lengthening of these cells is seen, especially at the chalazal end.

At the time of the four-nucleated stage of the germination of the megaspore the outer integument and pericarp are still present. Soon the outer integument begins to degenerate (fig. 4) and the pericarp shows signs of collapse. When the seed is nearly mature, the outer integument is gone, with the

pericarp persisting only as a thin layer, and the nucellus has been absorbed (fig. 5).

Mature seeds have a dark brown covering, two cells thick, formed from the inner integument. The pericarp is present only as a fibrous layer. The inner cells of the inner integument are rectangular in shape, with thick, hard walls. The outside cells have rounded walls, their outer walls being very much curved and thus forming the ridges seen on the seeds (fig. 6).

Seeds were gathered in October and kept in a warm, dry room in paper envelopes. An attempt to grow seedlings in the greenhouse in the winter was unsuccessful because the seeds

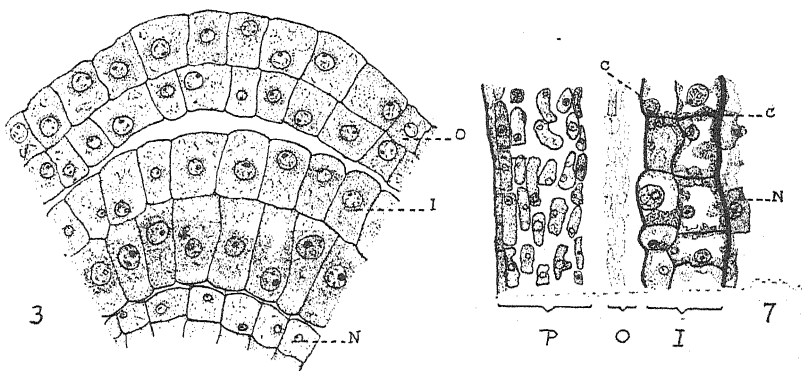


Fig. 3. Section of the outer and inner integuments, from an ovary of the same age as the one in fig. 2, showing the radial lengthening of the cells and darkening of the walls of the inner row of cells of the inner integument.

Fig. 7. Section through the seed coat with deposits of suberin or cutin shown by staining. C, cutin or suberin; symbols otherwise as in figs. 1, 2.

would not germinate. It was suspected that their failure to germinate was correlated with the character of the seed coat. Accordingly experiments on germination and microchemical tests of the seed coat were made.

In the experiments on germination certain methods and devices suggested by Crocker (3 & 4) were used. Dr. Eckerson's manual (5) and Tunmann's Microchemistry (14) were followed in making the chemical tests. Any tests depending upon color changes were difficult, because of the dark color of the seed coat, which resisted all attempts at bleaching.

In all the experiments on germination the seeds were placed on moist filter paper in crystallizing dishes. About thirty-five seeds were used in each lot treated, and the same number in a control in each case. The seeds used in the controls were gathered at the same time and kept as described before for the seeds used in the experiments, and therefore had not been affected by the forces of weathering. The experiments were

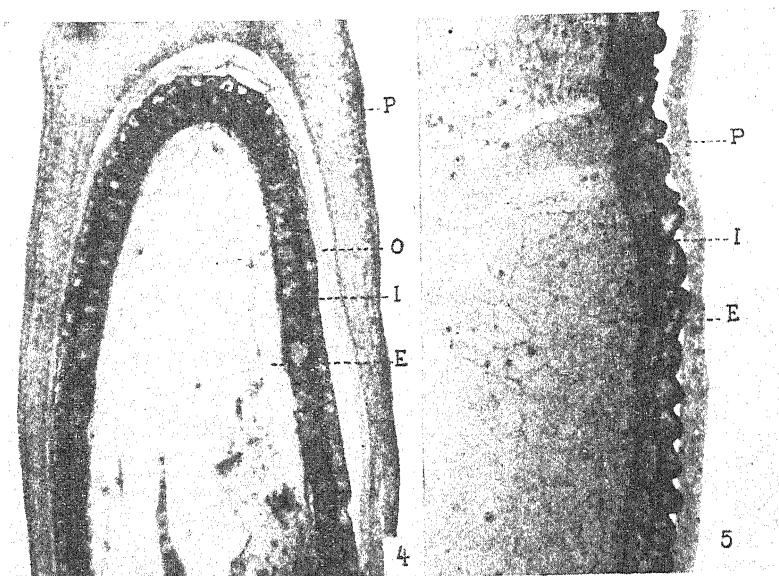


Fig. 4. Disintegrating outer integument. Fig. 5. Almost mature seeds showing the absence of the outer integument and the very thin pericarp. *P*, pericarp; *O*, outer integument; *I*, inner integument; *E*, endosperm.

started October 17 and the last one was performed January 21. Forcing agents suggested by Crocker (4) were used first.

Since some seeds will germinate after the seed coat has been scarified by some means, in the first experiment the seeds were rubbed between two pieces of fine sandpaper and placed in the germinating dish. In each of three lots so treated five or six seeds had germinated at the end of five days. One lot of seeds were mixed with sharp sand (about five hundred times as much sand as seeds), placed in a bottle, and shaken vigorously for

some time. Only one of these seeds germinated. Probably more would have germinated had the treatment been prolonged.

Since germination has been brought about thus far by physical changes, tests were made on the effects of freezing and thawing which seem to be of great significance in nature. Two different dishes were prepared. Each one was set outside on December 8. One was left outside a month. The other was brought inside three times during the month and placed near a radiator for two or three days. Thus it was subjected to great fluctuations in temperature,—from $-22^{\circ}\text{C}.$ to warm room temperature. The other seeds froze and thawed, but did not feel the great fluctuations in temperature. Both dishes were

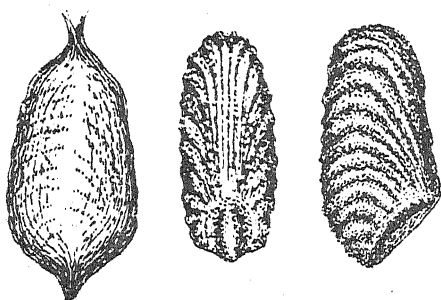


Fig. 6. Fruit and two views of the mature seed. Drawings made by Dr. Paul Weatherwax. $\times 25$.

brought in and placed near the radiator at the end of the month. After four days six seeds had germinated in each dish.

From previous experiments it seemed probable that the mechanical resistance of the seed coat might be such that the pressure of the expanding embryo could not rupture it without aid. Hence to test the mechanical resistance and to modify the colloids of the seed coat, the seeds were immersed in boiling water for one minute and then put to germinate. No results were obtained, either because the seeds were not in the water long enough or the temperature of the water killed the embryos.

Soil as a substratum frequently forces the germination of dormant seeds. Soil may contain a number of reagents which play a part, each acting upon the seed coat or upon living structures. Accordingly some seeds were placed on soil. At the end of a week one seed had germinated.

Seeds were immersed in an oxidizing agent, commercial hydrogen peroxide, and left for one-half day before being put to germinate. Not one germinated. Some other seeds were immersed in alcohol and left one-half hour before being put to germinate. None of these germinated. One lot of seeds were immersed in ether for ten minutes and another lot for forty minutes. After twenty days two seeds from the latter lot had germinated.

Near the middle of January some soil was taken from the place where *Eleusine* had grown the year before, and was kept moist in the greenhouse. In a week many seedlings appeared.

Seeds used in the controls carried on with these experiments gave uniformly negative results except in one case, where a single seed germinated. The fact that the seeds germinated from the very first if scarified showed that time for after-ripening was not necessary. Germination was delayed because of the nature of the seed coat. The need seemed to be for certain physical conditions rather than chemical stimuli.

Since the seed coats were found to be so hard that germination was impossible unless the seed coats were modified in some way, microchemical tests were made on the seed coat. The main parts of the seed coat seemed to be cellulose and suberin or cutin. Both Sudan III and a Scarlet R showed cutin or suberin present on the inner and outer surfaces of the integument and epidermis of the pericarp. In using either of these stains a drop of the solution was placed on the slide and after twenty minutes washed with 50 per cent alcohol (Eckerson, 5). The sections were then observed in glycerine. In using these stains, both the inner and outer surfaces of the integument and the epidermis stained red. The band of red on the inner surface of the integument was much thicker than that of the outer (fig. 7). A little red appeared in the cross walls which gave the appearance of suberin or some fatty substance. A chlorophyll solution (Harrington, 9) showed a tinge of green on the outer walls of the cells of the seed coat. This test was not satisfactory because the depth of the green could not be determined on account of the dark color of the seeds, but it seemed to indicate the presence of cutin or suberin in the outer walls. A solution of iodine (Strasburger & Hillhouse, 12) gave a starch reaction in almost all the pericarp. The degenerating outer integument

turned reddish brown, indicating a partial hydrolysis of the original cellulose. When an *Eleusine* slide was treated with iodine, washed well with distilled water, and 75 per cent sulphuric acid was added, the radial walls of the integument, the placenta, and a small part of the pericarp gave a cellulose reaction, turning blue or partly dissolving (Eckerson, 5). Immersing the seeds in concentrated sulphuric acid for six days caused the seed coats to become soft and brittle. On account of the black color added to the original dark color by these reagents it was impossible to tell what parts of the seed coat had been dissolved.

SUMMARY

In *Eleusine* the edge of the outer integument is not caught in the stylar canal as it is in most grasses. The integument continues on down to the micropyle and forms only a protuberance in the canal.

At the time of the four-nucleated embryo-sac the outer integument shows signs of absorption, giving the dextrin reaction, and at maturity it has been absorbed.

The inner integument completely surrounds the nucellus when the embryo-sac is mature. It consists of two layers of cells. The inner and outer surfaces of the integument are cutinized or suberized. The inner of these layers is much thicker. The cross walls are mainly cellulose.

The inner integument develops into a hard, grooved seed coat with the pericarp persisting only as a broken layer.

Seeds of *Eleusine* will not germinate until after the seed coat has been modified in some way. Failure to germinate apparently is not due to immaturity of the embryo. Freezing and thawing are natural forcing agents. Repeated fluctuations in temperature are not necessary. Scarifying the seed coat by different means gives good results in germination.

I take opportunity here to express my obligations to Dr. Paul Weatherwax for the suggestion of this problem and for assistance and criticism in connection with this study.

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New plants from Nevada

PHILIP A. MUNZ

During the past four seasons Mr. Edmund C. Jaeger of the Junior College at Riverside, California has made profitable trips to the Charleston Mountains in extreme southern Nevada. Among the very interesting plants that he and others have recently obtained in this isolated mountain range, the following species have been carefully studied and found worthy of description.

In this connection I wish to acknowledge my indebtedness to Dr. Ivan M. Johnston of the Gray Herbarium for kindly comparing these plants with material there, and to Dr. E. B. Copeland of the University of California Herbarium for loan of a collection of *Epilobium nivium* Brandeggee, namely one from St. Johns Peak, Lake Co., California, by W. W. Mackie in 1902, and for comparison of this loan with the type collection.

Lesquerella Hitchcockii Munz, n. sp. Perennial, silvery stellate throughout, stellae small with rays numerous and irregularly coherent; caudex much branched; stems ascending, 1-4 cm. long, unbranched; radical leaves varying from oblong or oblanceolate and with entire blades 5-8 mm. long, ca. 2 mm. wide, obtuse, and narrowed into slender petioles of same length, to broadly ovate or oblong, with blades 4-5 mm. long, 3-4 mm. wide, on somewhat shorter petioles; cauline leaves reduced, few, narrower; flowering stems 1-1.5 cm. long; subscapose, with terminal few-flowered corymbs; sepals 4-5 mm. long; petals pale yellow, linear-spatulate, 5-7 mm. long; filaments linear; fruiting stems 2-4 cm. long; fruits 3-8 in subcorymbose terminal cluster; pedicels stellate, ascending, not usually markedly sigmoid, 3.5-5 mm. long; capsules subglobose, not noticeably compressed, substipitate, reddish, glabrous, 3-4 mm. long, with entire septum; ovules 2-4 in each cell; styles filiform, reddish, 4.5-5 mm. long; seeds ca. 2 mm. long, brown, not winged.

Planta perennis, argenteo-stellata; foliis oblanceolatis aut ovato-oblongis, laminis 4-6 (8) mm. longis, 2-4 mm. latis; caulibus cum capsulis subscaposis, 2-4 cm. longis; floribus paucis, subluteis, corymbosis; capsulis subglobois, glabris, subrubris, substipitatis, 3-4 mm. longis; stylis 4.5-5 mm. longis; seminibus non alatis, ca. 2 mm. longis.

Type, fruiting plants from high exposed ridges in the Charleston Mountains of Nevada, at 10,500 ft. alt., collected by *E. C. Jaeger* and *C. L. Hitchcock*, Sept. 1, 1927 (Pomona College Herbarium No. 45092). An earlier collection in flower, same region, *E. C. Jaeger*, June 26, 1926 (Pomona). In the herbarium at Pomona College are two sheets from southern Utah with the smooth reddish fruits of the proposed species. One from Marysville, *M. E. Jones* 5404, has styles of same general length and rather narrower leaves. The second from Panguitch, *Jones* on July 18, 1920, has styles only 3 mm. or less long and narrow leaves. Both these plants are rather small and depauperate specimens, scarcely or not at all scapose, yet with the fruit of *L. Hitchcockii*. They differ from all other sheets I have seen from Utah, and indicate the need of more material from that region.

I take pleasure in naming this species for Mr. Charles Leo Hitchcock, one of my students, from whom more will be heard in Botany. The smooth fruits and low habit separate this species from others of the region.

***Draba Jaegeri* Munz & Johnston, n. sp.** Caespitose perennial; caudex often much and loosely branched; leaves more or less tufted, narrowly obovate, acutish to obtuse, 4–6 mm. long, 3–4 mm. wide, thickened and with indistinct midvein, pubescence rather loosely stellate, marginal cilia evident, leaves grayish but not silvery; scapes slender, pubescent, 2–5 cm. long; flowers showy, in a dense corymbose raceme 1–1.5 cm. long; sepals pubescent, purplish, hyaline margined, 2.5 mm. long; petals white, 5–6 mm. long; fruiting inflorescence not elongated; pedicels 4–6 mm. long; capsules flattened, densely stellate-pubescent, 4–6 mm. long, 3–4 mm. broad; styles filiform, 3–4 mm. long, dark; seeds brown, 1 mm. long, not winged.

Planta perennis, caespitosa; foliis cristatis, anguste obovatis, stellato-pilosis, ciliosis, 4–6 mm. longis, 3–4 mm. latis; scapis tenuibus, pubescentibus, 2–5 cm. longis; floribus spectabilibus; sepalis subpurpureis, pubescentibus; petalis albis, 5–6 mm. longis; pedicellis 4–6 mm. longis; capsulis complanatis, stellato-pubescentibus, 3–4 mm. latis; stylis 3–4 mm. longis; seminibus non alatis, 1 mm. longis.

Type, from Charleston Mts., in rock crevices at 11,000 ft. alt., *E. C. Jaeger*, June 26, 1926 (Pomona College Herbarium No. 44,771). A second collection from 10,000 ft. alt. by *E. C. Jaeger* was taken the same day (Pomona).

In Payson's key to the perennial scapose *Drabas* of North America (Amer. Jour. Bot. 4: 256. 1917) this species would be near to Payson's *vestita* (correct name, *D. Paysonii* Macbr.), but has leaves too wide. It might run also to his *D. Mulfordae*, from Idaho, but again the leaves are about twice as wide as in that species. The leaves and habit suggest *D. uncinalis* Rydberg, which is placed by Payson in the smooth-fruited species. He had not seen material for that species, but the co-type at Pomona College has ample pubescence on the fruits. The proposed species differs from *D. uncinalis* by its larger fruits and longer styles. In fact the very long styles set *D. Jaegeri* apart from all closely related species, exceeding even those of *D. pterosperma*, which differs by having winged seeds.

***Ivesia Jaegeri* Munz & Johnston, n. sp.** Green, perennial, villous and minutely glandular throughout, but not viscid; caudex woody, 2-3 cm. long, 7-8 mm. thick, crowned with persistent leaves and stems of previous years; stems several, slender, simple below, sparsely and openly branched above, spreading, ascending at tips, 2-15 cm. long; stipules 6-8 mm. long, the free portion 2-3 mm. long, lance-linear, entire; leaves pinnate, mostly basal; lower leaves with blades 1-5 cm. long; petioles 0.5-4 cm. long; leaflets 3-7 pairs, but not usually opposite, not crowded, 3-7 mm. long, divided almost to base into 3 or 4 oblanceolate to narrowly obovate segments, not bristle tipped, but frequently with 2-3 longer hairs at tips; upper leaves reduced, with 1-5 entire or somewhat divided segments, subsessile; flowers in 2-5 flowered open cymes; pedicels filiform, 0.5-2 cm. long; hypanthium saucer-shaped, 3-4 mm. wide; bractlets lanceolate, 2 mm. long; sepals ovate, 3 mm. long; petals yellow, narrow, oblanceolate, 2 mm. long, scarcely clawed; stamens 20, filaments linear, ca. 2 mm. long, seated close to the styles; receptacle hairy; pistils ca. 9; styles filiform, almost apical, ca. 2 mm. long; achenes brown, glabrous, scarcely 1 mm. long.

Perennis, viridis, villosus, vix glandulosus; caulibus aliquibus, tenuibus, subdecumbentibus, 2-15 cm. longis, ex caudice ligneo; foliis pinnatis, 1-5 cm. longis, cum 3-7 paribus pinnarum; pinnis 3-7 mm. longis, partitis, oblanceolatis aut anguste obovatis; floribus 2-5, in cymis laxis; hypanthio breve crateriformi, 3-4 mm. lato; sepalis ovatis, 3 mm. longis; petalis luteis, angustis, oblanceolatis, 2 mm. longis; staminibus 20; pistillis ca. 9; stylis linearibus, subapicalibus, 2 mm. longis; acheniis glabris, 1 mm. longis.

Type, Charleston Resort, Charleston Mts., July 3, 1927, *Marcus E. Jones* (Pomona College Herbarium No. 44, 277; isotypes at University of California, Gray Herbarium, and New York Botanical Garden). Known also from the following collections: limestone rocks, Charleston Mts., *Jaeger*, Sept. 12, 1925 (Pomona); at 10,000 ft., *Jaeger*, June 20, 1927 (Pomona); and Little Falls near Griffith's Resort, Kyle Canyon, Charleston Mts., *Jaeger*, Sept. 1, 1927 (Pomona). The species first came to my attention through the 1925 collection by Mr. Jaeger, and it is a pleasure to name it in his honor.

It is rather an interesting species in combining characters of *Ivesia* and *Potentilla* proper. Its general aspect is that of *Ivesia Baileyi* with foliage and habit like that species, but the number of stamens (20 instead of 5), the more filiform filaments, the position of the stamens near the pistils instead of being separated by an open space, and the rather subapical insertion of the style are more like *Potentilla*. The new species is less viscid-glandular than *I. Baileyi* or *I. setosa*.

***Epilobium nevadense* Munz, n. sp.** Low, suffruticose, caespitose, with freely branched woody caudex, these branches prostrate, dark brown, with freely exfoliating bark, and 2.5–3 mm. thick, giving rise to many slender, erect, pubescent, mostly simple stems, which are straw-colored, often purplish-tinged, 12–25 cm. high, leafy throughout; leaves glabrate, glaucescent, denticulate, green or purplish, on short pubescent petioles and tipped with inconspicuous stout rigid gland; lowerleaf-blades oblong, obtuse, opposite, 8–15 mm. long, 2–3 mm. wide, on petioles 2–3 mm. long; main cauline leaves alternate, somewhat narrower and more acute, gradually reduced upward, with fascicles of bract-like leaves in axils; leaves of inflorescence reduced to linear bracts 2–5 mm. long; flowers several on each stem, in loose racemes, sessile or on short glandular pedicel-like stems, each with small bract near base of glandular ovary; calyx tube glandular without, glabrous within, 2–3 mm. long, tinged reddish, tubular, slightly enlarged above ovary; calyx-lobes lanceolate, glandular, 3–5 mm. long, reddish, deflexed in anthesis; petals violet-purple, obcordate, 6–7 mm. long; stamens with filaments not dilated, the longer ones ca. 3 mm. long, shorter ones ca. 1.5 mm. long; anthers apiculate, 0.5 mm. long; style glabrous, ca. 10 mm. long; stigmas ca. 1 mm. broad, squarish in outline, with 4 subtriangular reflexed lobes; capsules subfusiform, glandular-pubescent, 8–12 mm. long, 1.5–2 mm. thick; the few seeds develop-

ing near the center, seeds smooth, brown, ca. 1.5 mm. long; coma white, about 5 mm. long.

Humilis, suffruticosa, caespitosa; ramis caudicis prostratis; caulibus tenuibus, erectis, pubescentibus, foliosis, 12-25 cm. altis; foliis glabris, glaucescentibus, denticulatis, linearibus aut suboblongis, 8-15 mm. longis, 2-3 mm. latis; pedicellis glandulosis; floribus in racemis; hypanthio glanduloso, 2-3 mm. longo, subpurpureo; lobis calycis lanceolatis, glandulosis, 3-5 mm. longis; petalis purpureis, obcordatis, 6-7 mm. longis; staminibus 1.5 aut 3 mm. longis; stylis glabris, ca. 10 mm. longis, stigmatibus quadrilobatis; capsulis subfusiformibus, 8-12 mm. longis, 1.5-2 mm. crassis; seminibus paucis, fuscis, 1.5 mm. longis; coma alba.

Type, from Cathedral Rock, Charleston Mts., Nevada, at 9200 ft. alt., Sept. 4, 1927, *E. C. Jaeger* (Pomona College Herbarium No. 152,780; isotypes at University of California and Gray). An earlier collection at 8000 ft. was made Sept. 12, 1925, *Jaeger* (Pomona). This interesting species is very close to *E. nivium* Brandege from Lake County, California. Both have the same general habit and stature; *E. nevadense*, however, has denticulate, glaucescent leaves rather than entire pubescent ones. The leaves are also narrower. *E. nevadense* has the flowers more glandular, and of different proportion, the calyx-tube being about half as long as in *E. nivium*, although the flowers are near the same general size. The coma is white instead of 'dingy'. The emphasis placed by Brandege on the stout, rigid gland at the apex of the leaves seems rather unwarranted, since this same structure (at most rather inconspicuous) occurs also in *E. nevadense* and *E. paniculatum*, to which annual species both *E. nivium* and *E. nevadense* are undoubtedly related.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1926-1929

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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A study of the genus *Clarkia*, with special reference to its relationship to *Godetia*

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During the past two years the junior author has been working under the direction of the senior on a revision of *Godetia*. During the progress of his study it was soon realized that a proper understanding of *Godetia* involved also the closely related *Clarkia*, especially so, since the latter name has priority and, if the two groups are congeneric, *Godetia* must be reduced. The present paper is written largely to discuss this situation. It is proposed to maintain *Godetia* as a genus, the North American species of which will be taken up in a separate paper by the junior author. In the present paper *Clarkia* is treated.

In carrying on the study here reported we have had available, material from:

Gray Herbarium of Harvard University (G),
Pomona College Herbarium (P).

The abbreviations indicated above are used in citing specimens. To Dr. B. L. Robinson and Dr. I. M. Johnston of the Gray Herbarium we hereby acknowledge our indebtedness and our appreciation of the many favors rendered. To Dr. W. L. Jepson of the University of California we are greatly obliged for the loan of the type of *Clarkia modesta* from his private herbarium.

HISTORY

The first species of *Clarkia* was published by Pursh, Fl. Am. Sept. 1: 260. *pl.* 11. 1814, as *C. pulchella*, being based on a collection by M. Lewis from the Kooskoosky and Clark's rivers, opposite the present town of Kamiah, Idaho. The generic name *Clarkia* was given in honor of Clark of the Lewis and Clark expedition. The next species was made known by Douglas in Lindl., Bot. Reg. 19: *pl.* 1575. 1833; this was *C. elegans*. Later followed *C. rhomboidea* Dougl., in Hook., Fl. Bor. Am. 1: 214. 1834, and other species.

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Table 1. Comparison of *Eularkia*, *Eucharidium*, *Phaeostoma*, and *Godeltia*

NAME	LENGTH OF HYPANTHIUM	INTERIOR OF HYPANTHIUM	PETALS	STAMENS	ANTHERS	SEED
<i>C. pulchella</i> (<i>EULARKIA</i>)	2-3 mm.	no band of hair, some hair at base of filaments	lobed, the blade 2-3 times claw	8, unequal, epipet- alous not func- tional	glabrate to cili- ate, coiling	cellular-pubescent, crest minute
<i>C. Xantiana</i> (<i>EULARKIA</i>)	2-4 mm.	band in upperpart, no hair on fils.	lobed, the blade 2-4 times claw	8, unequal, epipet. functional	ciliate, coiling	cellular-pubescent, little or no crest
<i>C. concinna</i> (<i>EUCHARIDIUM</i>)	15-25 mm., filiform	no band, no hair on filaments	lobed, the blade twice the claw	4; epipetalous gone	ciliate-villous, coiling	not cellular-pubes., transverse corru- gated; long crest
<i>C. Breweri</i> (<i>EUCHARIDIUM</i>)	25-30 mm., filiform	no band nor hair on filaments	lobed, blade 5-6 times the claw	4, clavate; epipet- alous gone	ciliate-villous, do not coil	as in <i>concinna</i>
<i>C. rhomboidea</i> (<i>PHAEOSTOMA</i>)	1-3 mm.	no band, hairy scales base of fils.	not lobed, blade 2-4 times the claw	8, unequal, all func- tional	glabrate, not coiling	cellular-pubes., scarcely crested
<i>C. elegans</i> (<i>PHAEOSTOMA</i>)	2-4 mm.	narrow band, & hair on dilated base epipet. fils.	not lobed, blade equaling claw	8, unequal, all func- tional	glabrate, scarcely coiling	cellular-pubes., scarcely crested
<i>C. delicata</i> (<i>PHAEOSTOMA</i>)	1-3 mm.	band in upper half, no scales or hairs on fils.	not lobed, blade 2-3 times claw	8, unequal, all func- tional	glabrate, not coiled	cellular-pubes., scarcely crested
GODETIA	1-15 mm., not filiform	narrow ring in lower or upper half, no scales	not lobed except in <i>G. biloba</i> ; blade at least 10 times as long as claw	8, subequal to un- equal, all func- tional	glabrate, not coiled	smooth except cell- pubes. in <i>epilobi- oides hispidula</i> , and <i>Whitneyi</i> ; crest, ex- cept in <i>epilobioides</i>

Eucharidium was proposed as a genus by Fischer and Meyer, Ind. Sem. Hort. Petrop. 2: 37. 1835, when they published *E. concinnum*. They described also *E. grandiflorum*, Ind. Sem. Hort. Petrop. 7: 48. 1840. *E. Breweri* was described by Gray, Proc. Am. Acad. 6: 532. 1865.

The genus *Phaeostoma* was created by Spach, Nouv. Ann. Mus. Paris III. 4: 395. 1835, and under *P. elegans* were included *Clarkia elegans* and *C. rhomboidea*.

Seringe, in D. C., Prodr. 3: 52. 1829, recognized *Clarkia* as a genus, and listed the only species known to that time, *C. pulchella*. Hooker, Fl. Bor. Am. 1: 214. 1834, included also *C. rhomboidea*. Spach l. c., restricted *Clarkia* to *C. pulchella*. Torrey and Gray, Fl. N. Am. 1: 515-6. 1840, recognized *Clarkia* and *Eucharidium* as genera, listing under the former: *C. pulchella*, *C. elegans*, *C. rhomboidea*, and *C. unguiculata*; and under the latter: *E. concinnum*. By them *Godetia* was included in *Oenothera*. Walpers, Repert. 2: 89-90. 1843, followed them in his generic concepts. Watson, Proc. Am. Acad. 8: 596-600. 1873, also included *Godetia* in *Oenothera*, but in 1876, in Bot. Calif. 1: 228-231, he recognized as genera: *Godetia*, *Eucharidium* and *Clarkia*. This was also the disposition by Raimann in Engler & Prantl, Nat. Pflanzenfam. 37: 212. 1893, *Phaeostoma* in both cases being included in *Clarkia*. Leveille, Monog. Onoth. 286-289. 1908, included all in *Oenothera*, and without any proper species concept. In 1911 Nelson, Bot. Gaz. 52: 267, revived the use of *Phaeostoma*, placing therein not only *P. elegans* and *P. rhomboidea*, but also *P. Xantiana*. Rydberg, Fl. Rocky Mts. 593. 1917, also recognized *Phaeostoma*. In 1918, Nelson and Macbride, Bot. Gaz. 65: 59-65, combined *Godetia*, *Phaeostoma*, *Eucharidium*, and the old *Clarkia* in one genus *Clarkia*, and created the new combinations necessary for many of the species. For the most part, however, the recent western manuals, such as those by Greene, Howell, Piper, and Jepson, have used two genera: *Clarkia* to include *Phaeostoma* and *Eucharidium*, and *Godetia* as the second.

DISCUSSION OF GENERIC STATUS

In the present discussion we are concerned with the four names mentioned in the previous paragraphs: *Clarkia* proper,

which for the purpose of clarity, we shall here refer to as Euclarkia, in which we include the species *C. pulchella* and *C. Xantiana*; Eucharidium, in which we recognize as species, *C. concinna* and *C. Breweri*; Phaeostoma, with *C. rhomboidea*, *C. delicata*, and *C. elegans*; and *Godetia*, with *G. biloba*, *G. epilobioides*, etc. The whole situation can perhaps be made most clear by a study of table 1.

It can readily be seen that characters do not vary together:

(1) Eucharidium, Euclarkia, and Phaeostoma agree in having the claws from one-fifth to one-half as long as the petals, the filaments and anthers usually quite unequal, the hair within the hypanthium lacking, or forming usually a fairly broad band. *Godetia* has claws less than one-tenth as long as the petals, the hair a narrow ring in the hypanthium, and the stamens subequal except in *G. epilobioides* and *G. purpurea*.

(2) Eucharidium and Euclarkia agree in their prominently lobed petals, irregular corollas, epipetalous stamens greatly reduced or quite aborted, and anthers usually hairy and coiling after dehiscence.

(3) Eucharidium stands apart in its long filiform hypanthium, entire suppression of epipetalous stamens, long crest and transverse corrugations on the seeds.

(4) Euclarkia and Phaeostoma agree in the short hypanthium, the eight stamens, cellular pubescence and minute cresting on the seeds.

(5) Phaeostoma and *Godetia* have little or no lobing, (except in *G. biloba*), epipetalous stamens functional, and anthers glabrate and not greatly coiled.

So far as we can see, these four groups represent three phylogenetic levels; the most primitive is *Godetia*, with little or no claws to the petals. It is most nearly related to *Oenothera* and has been included there by the earlier writers. The middle level is represented by Phaeostoma and Euclarkia, having the seeds of *Godetia* and the short hypanthium, but representing two lines of descent, Phaeostoma related to *Godetia epilobioides*, and Euclarkia to *G. biloba*. The upper level has Eucharidium, with its long filiform calyx-tube and crested corrugated seeds; it is evidently related to Euclarkia and continues certain tendencies there established, namely,

irregular corolla, lobed petals, and suppression of the epipetalous stamens.

With these phylogenetic levels in mind let us consider the various possibilities as to generic recognition:

(1) To recognize all four as genera. In so doing we get very much the same situation as has prevailed in *Oenothera*, of having a large number of none too distinct segregates with intergradation in so many directions as to make great confusion. In *Phaeostoma*, *C. delicata* and *C. rhomboidea* are near *Godetia epilobioides*; *Clarkia pulchella* and especially *C. Xantiana* are near *Godetia biloba*; and *C. pulchella* approaches *Eucharidium*.

(2) To combine *Phaeostoma* and *Euclarkia* in *Clarkia*, recognizing as other genera *Eucharidium* and *Godetia*. In many respects this arrangement is unsatisfactory, since *Eucharidium* and *Euclarkia* are evidently related, and since *Phaeostoma* and *Euclarkia* represent two distinct lines of descent.

(3) To merge all four in one genus *Clarkia*, perhaps the most consistent procedure taxonomically, but one that upsets a nomenclature well established in horticulture, since it requires giving up the name *Godetia*. After all, on the basis of clawed petals two groups can easily be distinguished.

(4) To combine *Euclarkia*, *Eucharidium*, and *Godetia biloba* in the genus *Clarkia* on the basis of prominently lobed petals, although *G. biloba* has a regular corolla and the others irregular ones; and to include *Phaeostoma* in *Godetia*, since both have quite entire petals. This arrangement seems quite artificial, separating *G. biloba* from its evident relative *G. Dudleyana*, and putting into *Godetia* *Clarkia elegans* with its highly specialized petals. Moreover this does away with the possibility of using a very characteristic feature, the narrow band of hair in *Godetia*, which breaks up in the others into various forms.

(5) To recognize two genera *Clarkia* and *Godetia*, placing the division between *C. rhomboidea* and *C. delicata* on the one hand, and *G. epilobioides* on the other, *C. Xantiana* and *C. pulchella* on the one and *G. biloba* on the other. These species might be variously transposed, but on the basis of claw-length, ring of hairs in the *Godetia* hypanthium, as contrasted with a band, total lack, or hairs about the base of filaments in *Clarkia*, and on the basis of stamen development, the line of division between the two genera seems best so. We there-

fore propose following Jepson, Man. Calif. 672-9. 1925, among recent authors, keeping up the name *Godetia* in the sense in which it has become so thoroughly established by usage. It is, therefore, largely on the basis of expediency and tradition, that we adopt this method, since other arguments for and against seem to us almost equally weighty.

CLARKIA

Clarkia, as a genus, Pursh, Fl. Am. Sept. 1: 260. *pl.* 11. 1814; Seringe, in DC. Prodr. 3: 52. 1829; Hooker, Fl. Bor. Am. 1: 214. 1834; Spach, Hist. Veg. Phan. 4: 392. 1835; T. & G. Fl. N. Am. 1: 515. 1840; Walpers, Repert, 2: 89. 1843; Benth. & Hook. Gen. Pl. 1: 789. 1847; Raimann, in Engler & Prantl, Nat. Pflanzenfam. 37: 213. 1898; Jepson, Fl. W. Mid. Calif. 277. 1911. (All references to this point do not include *Eucharidium*.) Greene, Pittonia 1: 140. 1887. Greene, Fl. Franciscana 223. 1891; Greene, Man. Bot. San Fran. Bay 136. 1894; Jepson, Fl. W. Mid. Calif. 331-332. 1901; Jepson, Man. Fl. Pl. Calif. 672. 1925. (This second group of references does include *Eucharidium*, as well as *Phaeostoma*.) *Clarkia*, included in *Oenothera*, Leveille, Monog. Onoth. 286. 1908. *Euclarkia*, subgenus, Jepson, Fl. W. Mid. Calif. 331. 1901. *Phaeostoma*, as genus, Spach, Hist. Veg. Phan. 4: 392. 1835; A. Nelson, Bot. Gaz. 52: 267. 1911; as a subdivision, rank not stated, Endlicher, Gen. Pl. 1192. 1840. *Opsianthes*, as genus, Lilja, Fl. Sverig. Suppl. 25. 1840. *Eucharidium*, as genus, Fisch. & Meyer, Ind. Sem. Hort. Petrop. 2: 36. 1835; T. & G. Fl. N. Am. 1: 516; Benth. & Hook. Gen. Pl. 1: 790; Engler & Prantl, l.c.; as subgenus, Jepson, l.c. *Clarkia*, including all these groups and *Godetia*, Nelson & Macbride, Bot. Gaz. 65: 59. 1918.

Annual herbs, simple or branched above, with spicate inflorescence and nodding or reflexed buds. Hypanthium short or greatly elongated; calyx-lobes distinct or united in anthesis. Petals distinctly unguiculate, claws at least one-sixth as long as blades; blades simple or lobed, pink to lavender or purplish. Stamens 4 and alternate with the petals, or 8, with the epipetalous ones shorter than the alternate and sometimes not functional. Anthers linear, fixed near the base. Stigma four-lobed, the lobes lance-linear to suborbicular. Capsule linear or attenuate above, 4-celled, usually 4-angled (at least when dried).

Seeds in one row in each cell, cellular-pubescent and with the creasing reduced, or not pubescent but with minute transverse corrugations and with conspicuous creasing.

Type species, *Clarkia pulchella* Pursh.

KEY TO SPECIES

Blade of petal lobed; corolla slightly irregular; anthers usually ciliate-villous.

Hypanthium 15-30 mm. long; stamens 4; seeds not cellular-pubescent, but transversely corrugated, and with conspicuous creasing.
(Subgenus *Eucharidium* (F. & M.) Jeps.)

Filaments club-shaped toward tips; anthers not coiling after dehiscence; middle lobe of petal much narrower than lateral ones; stigma lobes lance-linear, 3 mm. long. 7. *C. Breweri*

Filaments flattened but not club-shaped; anthers coiling after dehiscence; middle lobe of petals at least as wide as lateral ones; stigma lobes rounded, ca. 1 mm. long. 6. *C. concinna*

Hypanthium 2-4 mm. long; stamens 8; seeds cellular-pubescent, minutely crested. (Subgenus *Euclarkia* Jeps.)

Petals bilobed with subulate tooth at base of sinus; short stamens functional; hypanthium with ring of hairs within. California, from Kern County to Los Angeles Co. 4. *C. Xantiana*

Petals 3-lobed, lobes about equal; shorter stamens not functional; hypanthium without ring of hairs within. British Columbia to Montana and Oregon. 5. *C. pulchella*

Blade of petal not lobed, although occasionally with small teeth on the claw; corolla regular; hypanthium 1-4 mm. long; stamens 8, anthers glabrate; seeds cellular pubescent, scarcely crested

(Subgenus *Phaeostoma*).¹

Hypanthium without band of hairs or scales within; anthers curling slightly after dehiscence; blade of petal about as long as claw, the latter very slender. Mostly from coastal California, the length of the state. 3. *C. elegans*

Hypanthium with band of hairs within or with scales at summit; anthers not curling after dehiscence; blade of petal 2-4 times the length of the rather broad claw.

Calyx-lobes distinct in anthesis; scales present at base of filaments; capsule pedicelled; petals purplish. California, mostly from the interior, east to Arizona and Utah, and north through interior Oregon and Washington. 2. *C. rhomboidea*

Calyx-lobes united in anthesis; no scales on filaments, but band of hairs within the hypanthium; capsule nearly sessile; petals pinkish. E. San Diego Co., California. 1. *C. delicata*

¹ *Phaeostoma* (Spach) Munz & Hitchcock, n. subgenus. *Phaeostoma*, as genus, Spach, Hist. Veg. Phan. 4: 392. 1835.

TREATMENT OF SPECIES

1. *CLARKIA DELICATA* (Abrams) Nels. & Macbr. Bot. Gaz. 65: 60. 1918.—*Godetia delicata* Abrams, Bull. Torrey Club 32: 539. 1905; Jepson, Univ. Calif. Pub. Bot. 2: 352. 1907.

Simple to sparingly branched from the middle; stems 3–5 dm. tall, nearly glabrous; leaf-blades narrowly to broadly lanceolate, remotely to rather sharply denticulate, 2–5 cm. long, 0.3–1 cm. wide, acute to blunt, borne on very slender petioles 5–15 mm. long; flowers in long loose spike; inflorescence strigillose; buds nodding, obovoid, 5–10 mm. long; hypanthium 1–3 mm. long, with a band of hairs on upper half of inner surface; calyx-lobes united in anthesis, green or tinged reddish; petals spatulate, 1–1.5 cm. long, 5–7 mm. broad, the blade rose-pink, 2–3 times as long as the rather slender whitish claw; stamens 8, in two unequal sets; filaments filiform, the shorter epipetalous ones varying from three-fifths to nearly as long as longer ones; longer ones about half as long as petals; anthers glabrate, those of longer set reddish, 4–6 mm. long, tips very slightly recurved after dehiscence, shorter ones 2–4 mm. long, whitish, recurved after dehiscence; style equaling longer filaments; stigma-lobes rounded, 1–1.5 mm. long, equally broad, whitish; capsule 1.5–2.5 cm. long, 1.5–2.5 mm. thick, somewhat 4-angled when dry, nearly sessile, slightly beaked; seeds brown, cellular-pubescent, oblique-prismatic, 0.75 mm. long, not evidently crested.

Type locality, between Campo and Potrero, San Diego Co., California. Material seen,—CALIFORNIA, San Diego Co.: shady slope between Campo and Potrero, *Abrams 3710*, type coll. (C,² P, Stanford); San Felipe Creek, *Keck and McCully 104*, in 1925 (P); Barrett Dam, *Munz 8020* (P); Descanso T. S. Brandegee, May 24, 1906 (C), K. Brandegee, June 19, 1906 (C); top of grade, Descanso, K. Brandegee in 1906 (C); Ramona Ranch, T. S. Brandegee in 1906 (C); Potrero Grade, *Munz 9496a* in 1925 (P). Originally described under *Godetia*, this species quite breaks down any technical or adequate distinction between *Clarkia* and *Godetia*, but the spatulate character of the petals, the distinctness of the two sets of stamens, and the length of the claw are characters appertaining to *Clarkia*. Unpublished notes left by Mrs. Brandegee suggest concerning this plant: 'It has the appearance of a hybrid *Cl. rhomboidea*?

² C, abbreviation for University of California Herbarium, this material having come in a loan of *Godetia*.

× *G. epilobioides* and is in appearance nearer the latter.' To our way of thinking, it is a distinct species of rather local but natural range. We feel that enough collections have been made and over a period of enough years and from enough territory to preclude the possibility of its being a hybrid, especially since the characters exhibited are quite consistent. It is no doubt closely related to *Godetia epilobioides*, and represents probably an evolutionary step toward the more highly specialized *Clarkias*.

2. *CLARKIA RHOMBOIDEA* Dougl., in Hook. Fl. Bor. Am. 1: 214. 1834.—*C. rhomboidea* in T. & G. Fl. N. Am. 1: 516. 1840; Nels. & Macbr. Bot. Gaz. 65: 63. 1918. *Phaeostoma rhomboidea* A. Nels. Bot. Gaz. 52: 267. 1911. *Oenothera rhomboidea* of Leveille, Mon. Onoth. 287. 1908, in part. *Clarkia gauroides* Dougl., ex Sweet, Brit. Fl. Gard. ser. II, pl. 379. 1837. *Opsianthes gauroides* Lilja, Fl. Sverig. Suppl. 25. 1840. *Phaeostoma Douglasii* Spach, Nouv. Ann. Mus. Paris III. 4: 395. 1835, in part. *Godetia latifolia* Nels. & Kennedy, Proc. Biol. Soc. Washington 19: 156. 1906.

Plant simple or with few branches; stems 2–11 dm. tall, finely pubescent; leaves few, in well separated, almost opposite pairs, with a few secondary much reduced ones in the axils, upper ones single; blades lance-ovate to ovate-oblong or elliptic, 2–7 cm. long, 0.5–2 cm. wide, acute or blunt, entire or remotely denticulate, glabrate to finely pubescent, on slender petioles 1–3 cm. long; inflorescence rather sparsely strigillose; flowers borne in very few-flowered elongated spikes; buds nodding, ca. 1 cm. long, green; hypanthium 1–3 mm. long, obconic, bearing scales and white hairs at base of filaments; calyx-lobes green, generally distinct in anthesis; petals 5–10 mm. long, 3–6 wide, rose-purple, often lighter at base, sometimes dotted with purple; blade elongated rhomboidal, 2–4 times as long as the rather broad claw which is sometimes rather inconspicuously lobed or toothed at base; stamens unequal; filaments filiform, 3–5 mm. long, the longer ones bearing a slender hairy scale at base, the shorter ones half or nearly as long and with a shorter broader scale; anthers 2–4 mm. long, glabrous; style equalling longer filaments; stigma lobes rounded, ca. 0.5 mm. long, white to purple; capsules 1–3 cm. long, 2–4 mm. thick, 4-angled when dry, narrowed abruptly to a beak 1–4 mm. long, and borne on pedicels 1–4 mm. long; seeds brown, densely cellular-pubescent, prismatic, 1 mm. long, with a thickened ridge at the summit, cresting almost lacking.

Type locality, 'From the Great Falls of the Columbia to the Rocky Mountains,' collected by Douglas. Representative of the material studied,—WASHINGTON: Wenatchee region, *Brandegee* 780 (G); Spokane, *Kreager* 601 (G).—OREGON: Farewell Bend, Crook Co., *Leiberg* 482 (G,P); Blue Mts., Grant Co., *Henderson* 5634 (G); Eola, Polk Co., *Nelson* 4309 (G).—IDAHO: Ketchum, Blaine Co., *Nelson & Macbride* 1262 (G,P); Silver City, Owyhee Co., *Macbride* 379 (G); Pine Creek Valley, Latah Co., *Heller* 526 (G,P); Rush Creek, Washington Co., *Jones* in 1899 (P);—UTAH: East Bountiful, *Clemens* in 1908 (G); City Creek Canyon, near Salt Lake City, *Jones* 1838 (P).—NEVADA: Spooner, Douglas Co., *Baker* 1138 (G,P); Carson City, *Jones* in 1897 (P).—ARIZONA: Santa Catalina Mts., *Pringle* 269 (G).—CALIFORNIA: between Clear Creek and Paradise, Butte Co., *Heller & Brown* 5537 (G); Lakeport, Lake Co., *Munz* 9876 (P); Yosemite Valley, Mariposa Co., *Abrams* 4425 (G,P); Soda Springs, Nevada Co., *Jones* in 1881 (G,P); Kern River Canyon, Kern Co., *Abrams* in 1900 (P); Carmel River, Monterey Co., *Clemens* in 1910 (P); Los Angeles Co., Oakgrove Canyon, *Abrams & McGregor* 341 (G,P); San Antonio Canyon, San Gabriel Mts., *Johnston* 1404 (P); Forest Home, San Bernardino Co., *Feudge* 196 (P); Idyllwild, Riverside Co., *Spencer* 1367 (G P), Keen Camp, *Munz* 5771 (P); Mesa Grande, San Diego Co., *Spencer* 1155 (G,P); Vallecito Canyon, Laguna Mts., *Munz* 9712 (P); Sierra Valley, Sierra Co., *Hamlin* in 1904, type of *Godehia latifolia* (Nevada Exper. Sta.).

Clarkia rhomboidea has an unusually wide distribution, ranging from the interior of the Pacific States and adjacent Canada to the Black Hills of South Dakota, and to Arizona. Throughout its range it remains fairly constant, the chief variation being in the amount of the pubescence.

Greene's *C. virgata*, *Erythea* 3: 123. 1895, based on collections from Sonoma Co., California by *Bioletti*, and Amador Co., by *Hansen*, was characterized as 'cinereously puberulent throughout,' 'with long suberect, virgate branches rather densely floriferous throughout,' by rather thick, oblong-lanceolate leaves, and slender, scarcely incurved capsules. Material that fits this description is: Irishtown, Amador Co., *Hansen* 528, July 28, 1895 (P); and Agricultural Station, Amador Co., *Hansen* 528, July 1893 (G). A collection from Spooner,

Douglas Co., Nevada, *Baker 1138* (P), approaches these. The various characters assigned by Greene are so variable, and the entity so minor a thing that it does not seem worthy even of varietal rank, but may be regarded as *C. rhomboidea* forma *virgata* (Greene) Munz & Hitchcock, n. comb.

3. *CLARKIA ELEGANS* Dougl., in Lindl. Bot. Reg. 19: *pl.* 1575. 1833. *C. elegans* in T. & G. Fl. N. Am. 1: 515. 1840. *Phaeostoma elegans* Lilja, Fl. Sverig. Suppl. 25. 1840; A. Nels. Bot. Gaz. 52: 267. 1911. *Oenothera elegans* of Leveille, Monog. Onoth. 289. 1908. *Clarkia unguiculata* Lindl. Bot. Reg. 23: *pl.* 1981. 1837; T. & G. Fl. N. Am. 1: 516. 1840. *Phaeostoma Douglasii* Spach, Nouv. Ann. Mus. Paris III. 4: 395. 1835, in part. *Clarkia Eiseniana* Kell. Proc. Calif. Acad. 7: 94. 1877.

Plants simple or branched, 2–8 dm. tall; stems glabrous, glaucous; leaves gradually reduced up the stem; leaf-blades lanceolate to lance-ovate, 2–5 cm. long, 0.3–2 cm. wide, acute, remotely denticulate, glabrous, sometimes glaucous, sessile or narrowed into winged petioles 2–7 mm. long; inflorescence pubescent to glandular and pilose, especially the ovaries and calyces; flowers borne in long, loose spikes; buds deflexed, but not nodding, 1.5–2.5 cm. long; hypanthium 2–4 mm. long, campanulate, with a ring of hairs within about half way from the base, as well as additional hairs at the base of the stamens; calyx-lobes united in anthesis, often free at base in bud; petals rose to purple, 1–2 cm. long, 0.4–1 cm. wide, the blade deltoid-rhomboidal, about equal to very narrow claw; stamens in two sets, unequal; filaments 3–7 mm. long, the epipetalous ones the shorter and somewhat flattened, the alternate ones about as long as the petal-claws; anthers unequal, scarcely curling after dehiscence, alternate ones 6–8 mm. long, red or bright yellow, epipetalous ones 3–4 mm. long, white or pale yellow; style equaling or slightly shorter than longer stamens; stigma lobes short, rounded, 1–1.5 mm. long and about as broad, yellow; capsule 1–2.5 cm. long, ca. 2 mm. thick, sessile, beakless or almost so, usually glandular and pilose, but sometimes nearly glabrous, strongly curved to nearly straight; seeds brown, 1 mm. long, cellular-pubescent, possibly even glandular, angled on sides, with cresting very inconspicuous.

Type locality, California, based on material collected by Douglas. Representative of material studied,—CALIFORNIA: without locality, *Douglas*, probably type material (G); Oroville, *Heller 10767* (G); Mendocino Co., Ukiah, *Eastwood 3404* (G); Alpine School House, San Mateo Co., *Elmer 4293* (P); Napa,

Napa Co., *Dwight* in 1899 (G); Knight's Ferry, Sacramento Co., *Bigelow* in 1853-4 (G); Stanford University, *Abrams* 1655 (P); Santa Cruz, *Jones* 2255 (P); Ft. Tejon, Kern Co., *Abrams* & *McGregor* 307 (G,P); San Luis Obispo, *Palmer* 147 (G); Santa Monica Mts., *Abrams* 1711 (P); Azusa, *Gordon* (P); Valley Center, San Diego Co., *Feudge* 1712 (P); San Luis Rey, *Street* (P).

Individual specimens of this species are often difficult to distinguish from *C. rhomboidea*, so far as length of claw and petal-shape are concerned, although in the more typical condition and in well pressed specimens the characters are well marked. On the whole, *C. elegans* can be told by its campanulate rather than obconic hypanthium, united calyx-lobes, smoother glaucous stems, ovaries and buds usually with long spreading hairs, its more slender capsules, its longer stigma lobes, and the expanded hairy base of the epipetalous filaments rather than the presence of hairy scales at their base. *C. elegans* tends too, to have more and narrower leaves than does *C. rhomboidea* and they are less apt to be opposite.

For the most part, variation within this species is not sufficient to need special comment. There is a tendency, however, in some plants to lose much of the pilosity of the ovaries and buds; as examples may be cited: Kern River Canyon, *Abrams* 11990 and 12009 (P); Big Sandy Creek, Fresno Co., *McDonald* in 1915 (G); Three Rivers, Tulare Co., *Culbertson* 4208 (P). In some of these cases the same plant, in others, different plants in the same collection, may show no pilosity or a considerable development of it.

We have seen no authentic material of Kellogg's *C. Eiseniana* but the rather full description makes it seem quite certain that his plant was *C. elegans*. The long slender claw, the slender sessile capsule, and the 'hirsute' condition of the calyx-tube and calyx make this quite certain. We agree, therefore, with Mrs. Curran in reducing it to synonymy, *Bull. Calif. Acad.* 1: 137. 1885.

4. *CLARKIA XANTIANA* Gray, *Proc. Bost. Soc. Nat. Hist.* 7: 145. 1859-61. *Phaeostoma Xanthiana* A. Nels. *Bot. Gaz.* 52: 267. 1911. *Clarkia parviflora* Eastw. *Bull. Torrey Club* 30: 492. 1903. *Phaeostoma parviflora* A. Nels. l.c.

Simple or sparingly branched from near middle; stems 2-7 dm. tall, glaucous in appearance especially on lower portions where exfoliation of epidermis occurs, upper portions minutely strigillose; leaf-blades narrowly to broadly lanceolate, acute, entire to denticulate, sessile or with short petiole, finely pubescent to glabrate; inflorescence grayish-strigillose, flowers borne in a long loose spike; buds deflexed, 1-2 cm. long, tipped with a slender point 1-2 mm. long; hypanthium 2-4 mm. long, without scales but with a broad band of hair within; calyx-lobes 7-15 mm. long, usually united in anthesis, grayish green; corolla 'irregular, the two lower petals turned aside, the curved style protruding through the opening thus made'; petals lavender to rose, often with large spot of crimson or purple at base of blade, petals 1-1.5 cm. long, 0.6-1 cm. wide, cuneate, bilobed with small subulate tooth at base of V-shaped sinus, the lobes ca. $\frac{1}{4}$ the length of the whole petal, the claw broad, 3-4 mm. long; stamens 8, in 2 unequal sets, longer ones almost equal to petals, shorter ones ca. half as long; filaments subfiliform; anthers of longer set 4-7 mm. long, purplish, sparsely ciliate, those of shorter set 1.5-3 mm. long; style equalling petals, lavender or yellow; stigma-lobes short, rounded, 1-1.5 mm. long, yellow to purple; young ovaries deflexed; capsules erect, straight or curved, 4-angled, 1.5-3 cm. long, with beak ca. 1 mm. long or sometimes lacking, sessile or nearly so; seeds brown, obliquely cylindric, 1.5 mm. long, minutely cellular-pubescent, somewhat crested at angles.

Type locality, Fort Tejon, Kern Co., Calif. Material seen,— CALIFORNIA: Kern Co., Ft. Tejon, *Xantus de Vesey* 31, type (G), *Hall* 6306 (G,P), *Parish* 1898, in part (G), *Abrams & McGregor* 306 (G); Tehachapi, *Curran* in 1884 (G); Kern River Valley, *Coville & Funston* 1060 (G); Kern River Road, 15 mi. from Bakersfield, *Peirson* 7302 (P); Erskin Creek, *Purpus* 5538 (G); Big Rock Creek, Los Angeles Co., *Munz* 6879 (P), *Peirson* 7300 (P); Antelope Valley, *Oliver* in 1884 (G); Cucamonga Mts., San Bernardino Co., *S. B. & W. F. Parish* 952 (G).

The plants cited from the type region have somewhat larger flowers than those from the San Gabriel Mts. and from the Kern River region. It was apparently for these somewhat smaller flowered plants from the last named region that Miss Eastwood proposed the name *C. parviflora*. There is also considerable variation in the size and presence of the 'eye' on the petals, plants from the San Gabriel Mts. and even some from the type locality (*Hall* 6306) lacking it entirely.

5. *CLARKIA PULCHELLA* Pursh, Fl. Am. Sept. 1: 260. *pl.*
11. 1814. *C. pulchella* in T. & G. Fl. N. Am. 1: 515. 1840;
Spach, Nouv. Ann. Mus. Paris III. 4: 396. 1835; Nelson &
Macbride, Bot. Gaz. 65: 62. 1918. *Oenothera pulchella* of
Leveille, Monog. Onoth. 288. 1908. *Clarkia elegans* Poir.
in Dict. Sci. Nat. 9: 355. 1817.

Plant simple to diffusely branched, 10–50 cm. tall; stems and inflorescence finely pubescent to strigillose, very leafy; upper leaves not much reduced; leaf-blades linear-lanceolate to spatulate, sessile or with petiole as much as 1 cm. long, entire or remotely denticulate, 2–7 cm. long, 0.2–1 cm. wide, acuminate to acute or lower ones obtuse; flowers in a short crowded spike which elongates in fruit; buds nodding, 1–2 cm. long, green to lavender, usually tipped with slender point 1–2 mm. long; hypanthium 2–3 mm. long, lavender, without hairs within; calyx-lobes usually united in anthesis, 1–1.5 cm. long, lavender; petals orbicular-obovate in outline, lavender to purple with lighter veins, 1.5–3 cm. long, 1–2.5 cm. wide, 3-lobed, the lobes 6–10 mm. long, about equal in length, but with middle one usually wider than lateral ones, claw quite narrow, one-third to one-half as long as blade, with a divaricate tooth on each side about one-third way from base, stamens 8, in two sets, the epipetalous ones small, scarcely if at all functional without scales at base, the longer ones 3–8 mm. long with erect sparsely pubescent scale at base; anthers yellow, coiling after dehiscence, longer ones 3–5 mm. long, shorter ones one-fourth as long; style equaling to slightly exceeding longer stamens; stigma lobes rounded, 1–3 mm. long, whitish; capsule 1–2.5 cm. long, scarcely beaked, straight to strongly curved, 8-ribbed, grooved on each face, appearing square when dried, borne on pedicel 3–10 mm. long; seeds brown, cellular-puberulent, depressed, oblique, not angled, 1 mm. long, with minute crestring.

Type locality, 'Opposite the town of Kamiah, Idaho,' on the Kooskooskee River. Representative of material seen,—BRITISH COLUMBIA: near Int. Bound., between Kettle and Columbia Rivers, *Macoun 64, 602* (G,P).—WASHINGTON: Spokane, *Kreager 15* (G); Colfax, *Jones* in 1911 (P); Pullman, *Eastwood 13142* (P).—OREGON: Portland, *Jones* in 1902 (P); Mt. Hood, *Jones* in 1897 (P); the Dalles, *Davidson* in 1885 (P).—IDAHO: St. Mary's River, *Leiberg 1090* (G,P); Moscow, *Abrams 713* (P); Boise City, *Wilcox* in 1881 (G).—MONTANA: Big Fork, *Jones 8401* (P); Evaro, *Jones* in 1909 (P); Ravalli, *Jones* in 1909 (P).—SOUTH DAKOTA: Black Hills, *Forwood* in 1887

(G). Introduced into the eastern United States, as, VERMONT: Rochester, *Dutton* in 1914 (G).—MASSACHUSETTS: Lexington, *Piper* 3230 (G).

6. *CLARKIA CONCINNA* (F. & M.) Greene, *Pittonia* 1: 140. 1887.—*Eucharidium concinnum* Fisch. & Meyer, *Ind. Sem. Hort. Petrop.* 2: 37. 1835; T. & G. *Fl. N. Am.* 1: 516. 1840. *Eucharidium grandiflorum* F. & M. *Ind. Sem. Hort. Petrop.* 7: 48. 1840. *Clarkia grandiflora* Greene, *Fl. Francisc.* 223. 1891.

Plant simple to freely branched, 1.5–4 dm. tall; stems glabrate below and strigillose toward summit; leaf-blades lance-ovate to broadly elliptic, 1.5–5 cm. long, 0.3–2 cm. broad, acute to blunt, nearly entire, borne on slender petioles 0.5–2 cm. long, glabrate; flowers in upper axils often crowded; buds usually nodding, purplish or green, 1–2 cm. long exclusive of hypanthium, tipped with a very short point; hypanthium 1.5–2.5 cm. long, very slender, scarcely widened at summit, slightly swollen at base, yellow to purple, finally pubescent within, especially at base of filaments, but without scales or band of long hairs; calyx-lobes reddish, sometimes green, 1–2 cm. long, united at tips in anthesis, lower half of the inner surface orange to red, terminal portion reflexed; petals 1.5–3 cm. long, 1–1.5 cm. wide, deep pink to rose lavender, purplish on drying, central portion paler, blade about twice as long as claw, three lobed, central lobe spatulate to obovate and slightly exceeding lateral lobes in length and width, 'the three upper petals approximate, the fourth slightly declined'; stamens 4, alternate with petals; filaments slightly flattened, not dilated at base, 5–7 mm. long, lavender or purple; anthers 3–4 mm. long, purplish, ciliate-villous, curled after dehiscence, 'upper anthers extrorse, lower anthers introrse, the opening of all thus facing upper lip of corolla'; style equaling stamens; stigma lobes ca. 1 mm. long, equally broad; capsules 1.5–2.5 cm. long, 1.5–2.5 mm. thick, 4-angled when dried, sessile or on short pedicels, tapered gradually to a beak 1–3 mm. long; seeds minutely transversely corrugated, ca. 2 mm. long, flattened, with very prominent crestring.

Type locality, Ft. Ross, California. Representative material,—CALIFORNIA: Hupa Indian Reservation, Mendocino Co., *Chandler* 1325 (G); Kenwood, Sonoma Co., *Michener & Bioletti* in 1893 (P); near Alder Springs, Glenn Co., *Heller* 11457 (G); Vaca Mts., Napa Co., *Jepson* in 1891 (G); Lakeport, Lake Co., *Munz* 9871 (P); Berkeley, Alameda Co., *Blankenship* in 1892 (G); Oakland, *M. E. Jones* in 1881 (P);

Bolinas Ridge, Marin Co., *Palmer 2407* (P); Steven Creek, Santa Clara Co., *Pendleton 755* (P); Santa Barbara Co., *Torrey 94* (G).

So far as we can judge, *C. grandiflora* falls well within the natural variation occurring in a fairly large number of specimens of *C. concinna*.

7. *CLARKIA BREWERI* (Gray) Greene, *Pittonia* 1: 141. 1887.—*Eucharidium Breweri* Gray, *Proc. Am. Acad.* 6: 532. 1865. *Clarkia Saxeana* Greene, *Pittonia* 1: 140. 1887.

Simple or branched, 10–20 cm. tall, stems finely pubescent; leaf-blades lanceolate to oblong-lanceolate, 2–4 cm. long, 0.3–0.6 cm. wide, acute, entire, glabrate, on petioles 5–10 mm. long; inflorescence sparsely strigillose, flowers few; buds nodding, 1–2 cm. long, greenish, abruptly narrowed to a point 1–3 mm. long; hypanthium 2.5–3 cm. long, conspicuously swollen at juncture with ovary, finely pubescent within but lacking scales or band of hairs; calyx-lobes reddish or green, united in anthesis; corolla rose-pink, irregular, the two lower petals bent downward, each petal strongly obcordate with the central lobe merely a spatulate appendage from the sinus and one-third to one-fourth as wide as the lateral lobes, petals 1.5–2.5 cm. long, almost as wide, the sinus 4–6 mm. deep, claw 3–4 mm. long; stamens 4, equal, alternate with petals; filaments 1–1.5 cm. long, somewhat flattened and greatly dilated at summit; anthers 4–7 mm. long, conspicuously ciliate-villous, lavender or red, erect, not coiled after dehiscence; style equaling or slightly exceeding stamens; stigma lobes lance-linear, 3 mm. long, ca. 1 mm. broad; capsule 2–3.5 cm. long, 2–3 mm. thick, tapering to a slender beak 2–4 mm. long, sessile; seeds 3 mm. long, not pubescent, but conspicuously transversely corrugated, brown, flattened, with very prominent creasing.

Type locality, 'dry summit of Mount Oso, at elevation of about 3200 ft.' in Stanislaus Co., California. Material seen,—CALIFORNIA: headwaters of the San Benito River, San Benito Co., *Hall 9939* (P); Emmett to Panoche Pass, San Benito Co., *Abrams & Borthwick 7903* (P); Mt. Oso, Stanislaus Co., *Brewer 1247*, type (G); Cerro Bonita Mine, Panoche, Fresno Co., *Gilmore* in 1878 (G); Geysers, Napa Co., *Dr. Saxe*, type material of *C. Saxeana* (G).

The two remarkable features of this species are the clavate filaments and the narrow median lobe of the petals. Greene's description of *C. Saxeana* fits *C. Breweri*, and authentic material at the Gray Herbarium which was sent in 1888 to Dr. Watson

by Mrs. Curran from the California Academy Herbarium makes the identity of the two species certain.

UNCERTAIN OR EXCLUDED SPECIES

1. *CLARKIA MODESTA* Jepson, Man. Calif. 673. 1925. The type of this species from Waltham Creek, San Carlos Range, California, *Jepson 2690*, has been loaned us through the kindness of Professor Jepson. It agrees perfectly with *Heller 11458* from ten miles east of Alder Springs, Glenn Co. (G), in the shape of petals, stamens, ring of hair in uppermost portion of hypanthium, slender capsules, and all other features so far as we can discover. The Heller collection and other plants from central California, such as: *Bigelow* in 1853-4 from Knight's Landing, Sacramento Co. (G); *Congdon* in 1895 from Lewis, Mariposa Co. (Stanford); and *K. Brandege* from Antioch, Contra Costa Co. (Stanford) are being referred to *Godetia epilobioides* in the paper by the junior author. From some material of *G. epilobioides* they differ in the somewhat narrower pink petals, but in the southern part of the range every degree of intergradation has been found. The claw is no longer than on the broader petals of typical *G. epilobioides*.

2. *GAUOPSIS LANCIFOLIA* Presl, Epim. Bot. 219. 1849, from Mexico was referred by Leveille, Monog. Onoth. 287. 1908 to his *Oenothera rhomboidea* (*Clarkia rhomboidea* Dougl.). So far we have been unable to get material or information which enables us to arrive at any decision concerning *Gauopsis lancifolia*.

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Notes on the marine algae of Florida

WM. RANDOLPH TAYLOR

(WITH TWO TEXT FIGURES)

In closing the manuscript of his report upon the Florida marine algae the writer (1928) felt that he had incorporated the great majority of the species which could confidently be assigned to the state, and that the catalog was essentially complete. However, there remained a considerable number of reports that seemed inadequately confirmed or otherwise improbable, and the further possibility that a search of the scattered literature on the algae of South America and the Caribbean Sea might yield others. The labor involved in searching upwards of 150 papers bearing directly upon this territory for possible Florida records would not soon have been justified had not a very considerable amount of undetermined West Indian and Brazilian material come into the writer's hands for study. This forced him into the preparation of a catalog of the algae of the entire western tropical Atlantic Ocean, and naturally brought to light some previously unconsidered Florida reports. While very few of these are to be accorded much confidence, it is distinctly worth while to bring all of them together and to indicate their probable importance to the catalog of the algae of the state. The additions are not so much directly derived from earlier publications as from comparatively recent and important papers, items from which were withheld from the original Florida report for various reasons. Eighteen names are here definitely added to the flora, giving a total of 478 different algae, of which 62 are forms and varieties of species also present in the typical condition. In addition consideration is given here to 28 names which do not appear to be sufficiently well known (as representing Florida plants) to justify inclusion at this time, but which cannot be reduced to synonymy.

The Guadeloupe flora has long been held to be by far the richest recorded for the West Indies or indeed anywhere near the Atlantic coast of the Americas. That this impression is far from correct has long been clear to the writer. While thoroughly studied in the field, the flora as represented by the catalog of Mazé & Schramm (1870-77) involves so many obsolete names, *nomina nuda*, and incorrect determinations that it cannot now

be accepted as presented. It appears that somewhat over 250 species well recognized in the West Indies can be directly associated with names they use. In addition somewhat over 290 species names are doubtful, since inadequately confirmed in the literature, but have not been reduced to synonymy under the familiar West Indian species. The distinctions between these groups being at present largely based on the writer's personal opinion, the relative numbers are subject to change.

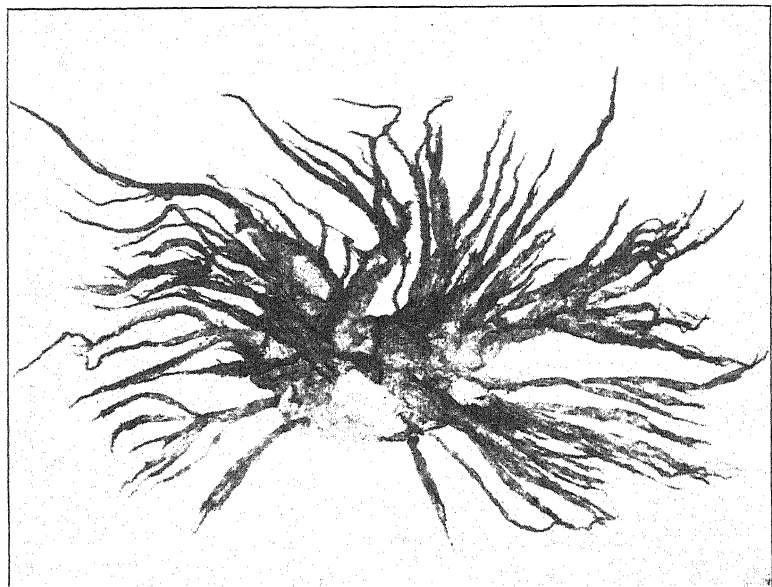


Fig. 1. Habit of typical specimen of *Hydrocoleum penicillatum*, $\times 0.95$. The more delicate filaments which extend beyond the general mucous mass of the erect branches of the thallus do not appear distinctly in the reproduction.

The rest of their nearly 800 marine algal names (excluding diatoms) are either reduced to synonymy or (in a small proportion) apply to varieties and forms also represented by the typical condition. In comparison with the Florida flora of nearly 420 well authenticated species we have a Guadeloupe flora of about 250 species very probably present, and a residue of about 290 names from which additions will be possible when a review of the original material allows accurate disposition of the records to be made. The descriptions of new species are too inad-

equate to be of much assistance, and many of the records are very improbable indeed. At the time of the preparation of the Florida algae report it was not possible to analyze suitably the Guadeloupe records, so this opportunity is taken to point out the present state of our knowledge. As was indicated there, the recorded algal flora of none other of the West Indies appears as rich as the coast of Florida.

The writer desires to express his indebtedness to Dr. M. A. Howe of the New York Botanical Garden for much kind assistance and for access to the algal collections of the Garden. The herbarium of John Hooper was examined for Florida algae through the kindness of the Brooklyn Botanic Garden.

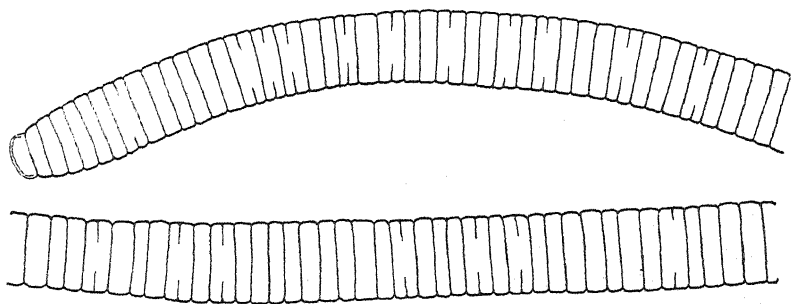


Fig. 2. Apex and more median portions of trichomes from *Hydrocoleum penicillatum*, $\times 900$, approx. As prepared from dried material, the sketch probably overemphasizes the degree of constriction of the trichome at the cell junctures.

ADDITIONAL RECORDS

Hydrocoleum penicillatum n. sp. Plant forming an expanded layer, little colored, mucous but including calcareous sediment or perhaps partly calcified; from this arise abundant fasciculate projections usually about 3.0 cm., but reaching 5.0 cm. tall and 2.0 mm. in diameter, simple or with 1-10 main branches, mucous and pale below, above increasingly pilose with dark brown-violet filaments, the ends more or less penicillate and attenuate; trichomes $9.5-(11.1)-14.3\mu$ in diameter, cells $1.9-(2.8)-3.8\mu$ long; trichomes obviously calyptrate, calyptra depressed rounded and pale straw color to nearly colorless; trichomes hardly capitate, slightly tapered near the apex which is nearly straight, slightly constricted at the transverse walls which are inconspicuously and rarely granulated; sheaths highly confluent, the individual ones hardly recognizable. (Figs. 1, 2.)

The above description was based upon dried material moistened with lactic acid and glycerine before mounting in water for microscopic study. Since the limits of the sheaths could not be made out clearly, no decision could be reached as to the number of the filaments within a sheath. There was noted a strong tendency toward a longitudinal fracture of the filaments which did not disappear on soaking, and this gave a confusing impression of trichome diameter until recognized from the exact correspondence of the transverse walls on opposite sides of the split and the relation to the apical region of the filament. In the central portions of the mounts the material appears to have dried somewhat too slowly and there was discharged onto the paper a brilliant pink pigment, leaving the specimens bright green. This is, of course, not unusual in Myxophyceae which contain pink pigments. In *Hydrocoleum* this plant would come nearest to *H. lyngbyaceum* on the basis of trichome size, and in part also on the extremely diffuent character of the individual sheaths, but differs conspicuously in the habit assumed and also in having rather shorter cells, no conspicuously capitate apex and the violet color. In this last respect it resembles *H. comoides*, but there is little else in common between them.

The station for the material is given as South Shore near Battery and south of Old Fort, Key West, Florida; collected by R. Thaxter, Feb. 1898; type material in Farlow Herbarium, Harvard University.

LYNGBYA LUTEA (C. Ag.) Gom. This plant is attributed to Florida by Tilden (Minnesota Algae 1: 115) and is similarly accepted by Hoyt (1920). As the plant occurs in North Carolina and is reported in the West Indies, the Florida record is not improbable. (p. 44).¹

MICROCOLEUS CHTHONOPLASTES Thuret ex Gom. A collection of this species made by R. Thaxter at Cocoanut Grove, Florida, 1898-99, has been seen by the writer and the determination appears to be correct. Associated were *Lyngbya confervoides* and indeterminate Chroococcaceae. The habitat was perhaps brackish rather than completely marine. (p. 45).

MONOSTROMA LATISSIMUM (Kg.) Wittr. Collins (1909) records this species from Florida, and Collins & Hervey (1917) from Bermuda. (p. 56).

¹ Page references are to the writer's report on Florida algae (1928).

ULVA FASCIATA Delile. Collins (1909) records this species from Florida. As it is common and widespread in the American tropics, the record is probably correct, and material in Curtiss' *Algae Floridanae* at the New York Botanical Garden appears to be this species, collected at Oceanus in 1896. (p. 57).

ULVA LACTUCA L., var. *LATISSIMA* (L.) DC. Specimens of this variety from Key West, Florida, have been seen by the writer, especially those in the Farlow Herbarium collected by 'B. M. W., Sta. 26, June 19, 1893.' This appears to be a new record. (p. 57).

CHAETOMORPHA CLAVATA (C. Ag.) Kg. Collins (1909) lists this plant from Florida. As it is known from the Bahamas and the outer West Indies the record is probably correct. (p. 60.)

HALICYSTIS sp. A member of this genus has been reported by Blinks (1927) as present at Bermuda and Florida (Dry Tortugas), without assurance as to the specific determination. The writer has Bermudan samples of this material, and agrees in the disposition of it.

STRUVEA PULCHERRIMA (J. E. Gray) Murray & Boodle. Collins (1909) mentions the finding of a fragment of this plant by Mrs. Hall at Jupiter Inlet, Florida, as being only a second record. The original plant (also a fragment, though larger) was dredged in the Gulf of Mexico by Menzies. The record is probably correct, since the plant is very distinctive, although excessively rare. (p. 74.)

RHIZOCLONIUM RIPARIUM (Roth) Harv. While Collins (1909) does not attribute this plant to Florida, Hoyt (1920) does consider that it occurs there. Since it appears in the Bermudas and Bahamas, it probably is present in Florida also. (p. 66.)

BRYOPSIS RAMULOSA Mont. This is reported from Florida by Collins (1909). (p. 93.)

GELIDIUM CRINALE (Turn.) J. Ag. Excellent specimens of this plant are to be found in the New York Botanical Garden Herbarium, collected at St. Augustine, Florida, by Mrs. G. A. Hall, and from St. Augustine Inlet by A. H. Curtiss in April 1897. (p. 142.)

COTTONIELLA FILAMENTOSA (Howe) Børg. This plant is described from Florida by Howe (1905b). (p. 162).

CHONDRIA CNICOPHYLLA Melv. This plant was described

from western Florida by Melvill in Murray (1889), and the record is so far to be accepted. (p. 170.)

LAURENCIA GEMMIFERA Harv. This species was described from Florida and the record was accepted by Murray (1889) and more recently by Howe (1920). Plants belonging under this name were secured by the writer from Key West and Dry Tortugas, the omission from his text (1928) being an oversight. At Dry Tortugas *L. gemmifera* was obtained at Bird, Loggerhead, and East Keys from the sublittoral to a depth of 6 meters, appearing to be primarily a plant of shallow, quiet, strongly illuminated water. It most resembles forms of *L. obtusa* or of *L. Poitei*, being distinguishable by the turgid or papillate contour of the epidermal cells near the apices of the branches. (p. 179.)

ANTITHAMNION PLUMULA (Ell.) Thuret. Specimens of this plant have been seen by the writer in the Farlow Herbarium, purporting to have been dredged off Key West, Florida. This appears to be a new record, and a very considerable extension of the American range. (p. 188.)

LITHOPHYLLUM BERMUDENSE Fosl. & Howe. A record of Florida material by the authors of the name (1906) is to be accepted. (p. 209.)

LITHOTHAMNIUM FLORIDANUM Fosl. Foslie (Algol. Not. 2: 11. 1906) and DeToni (Sylloge Algarum 4: 1782) accord this plant to Florida. (p. 209.)

DOUBTFUL RECORDS

ENTEROMORPHA COMPRESSA (L.) Grev. Murray (1889) records this plant from Florida on the basis of a report by Melvill (1875) and on Harvey's statement that its distribution is general in North America. Collins (1909) does not grant a more southerly range than New Jersey. (p. 55.)

ENTEROMORPHA RAMULOSA (Eng. Bot.) Hooker. Collins accepts this plant (1909) as occurring from New England to the West Indies; Hoyt (1920) does not mention it, but DeToni (Sylloge Algarum 1: 134) assigns it to Florida. On the whole, the Florida record is not well confirmed. (p. 56.)

CLADOPHORA PROLIFERA (Roth) Kg. Hooper (1850) reports this species from Florida, but his determinations deserve little confidence. Collins (1909) does not accept the record;

perhaps the plant was *C. fuliginosa* or *Cladophoropsis*. However, records from farther south do appear to be correct. (p. 64.)

CAULERPA COCCINIA. Hooper (1850) lists a plant under this name, but the writer has been unable to determine what he had in hand, or to locate any other use of the name.

CAULERPA TAXIFOLIA (Vahl.) C. Ag. Børgesen (1913) lists this plant from Florida, but without particular explanation. Collins (1909, 1912, 1918) does not accept the record, nor does it appear in other places where it would be expected. While the plant is found in the outer West Indies and even Bermuda, and so is to be expected in Florida, it is best to hold the Florida record in question until more specific information on the local specimens is available. (p. 103.)

ASPEROCOCCUS CLAVATUS. This record by Hooper (1850) for Florida is unconfirmed, and is probably incorrect. The significance of the name, at least, is not clear. (p. 110.)

ASPEROCOCCUS ECHINATUS (Mert.) Grev. This record by Hooper (1850) is unconfirmed, and is probably incorrect. The species is a north-temperate one. (p. 110.)

CASTAGNEA VIRESCENS (Carm.) Thuret. Hooper (1850) and Farlow (1876) both list this species, but the records are probably incorrect (Taylor 1928, p. 113). An examination of a specimen from Garden Key in the Collins Herbarium at the New York Botanical Garden showed sporangia up to 44μ in diameter. Since the plant was a sturdy one, somewhat suggesting *C. virescens*, measurements were made of sporangia on slides of New England *C. virescens* sectioned in celloidin, where the sporangia were found to reach 66μ in diameter and 95μ in length. From this and other features of structure it seems best still to consider all of the Florida material to be *C. Zosteræ*. (p. 113.)

PADINA COMMERSONII Bory. Murray (1889) lists this plant from Florida, but the record is to be considered very doubtful. Perhaps it was based on juvenile material of *P. Sanctæ-Crucis*. (p. 123.)

PADINA PAVONIA (L.) Gaill. This species has been reported from Florida and for several of the West Indies by Murray (1889). Collins (1917) in announcing its presence at Bermuda emphasized the unreliability of the older records. There is no reliable record of its presence on the Florida coast. (p. 123.)

CYSTOSEIRA ERICOIDES Goodw. & Woodw. Hooper (1850) lists this plant, but there is no confirmation of its presence in Florida or elsewhere in the American tropics. (p. 126.)

SARGASSUM DENTIFOLIUM (Turn.) C. Ag. Murray (1889) assigns this species to Florida, but there is no other record beside that of Farlow (1876), on which Murray's is probably based. Perhaps Farlow had *S. pteropleuron*; at any rate the report is very doubtful. (p. 127.)

ACROCHAETIUM VIRGATULUM (Harv.) J. Ag., var. LUXURIANS (J. Ag.) Rosenv. Murray (1889) accords this variety, under the name of *Callithamnion luxurians* J. Ag., to Florida on the basis of Melvill's collections. The plant under the latter name in Harvey (1853) does certainly appear to be an *Acrochaetium* but is not there listed from Florida. As old determinations in *Acrochaetium* are often untrustworthy it is best to hold the Florida record in question. (p. 134.)

HELMINTHOCLODIA CALVADOSII (Lamx.) Setch. Murray (1889) accepts reports of this plant under the name of *H. divaricata*. Murray, Collins & Hervey (1917), and Howe (1918) accept the plant as present at Bermuda. However, as there is no direct confirmation of Melvill's (1875) report of the plant in Florida, the record may best be held in question. (p. 135.)

SCINAIA FURCELLATA (Turn.) Bivona. The Florida report of the species comes from Harvey (1853) through Murray (1889). The material very probably will be found to be *S. complanata*, which is the tropical species, while *S. furcellata* is found in more northern and colder waters. (p. 141.)

STENOGRAMME INTERRUPTA Mont. The Florida material passing under this name seems to consist of a sterile fragment found by Harvey (1853) at Key West. While reproducing plants are quite characteristic, the sterile plants are much less so, and in view of the character of the material and the absence of other records from the American tropics it is best to consider the record as very doubtful. (p. 147.)

GRACILARIA ARCUATA J. Ag. Mention of this species from Florida appears in DeToni (Sylloge Algarum 6: 259). As the only other record from the American tropics appears in Mazé & Schramm (1870-77) and may not be based on similar material, the Florida report is ill confirmed and may be held in doubt. (p. 151.)

GRACILARIA ARMATA (C. Ag.) J. Ag. This plant is reported from Florida by Harvey (1853), but it is characteristically European. There are several other, but not very convincing, reports from the American tropics. Of these the one accepted by Murray (1889) from Kemp and Rein for Bermuda is attributed by Collins & Hervey (1917) to *G. ferox*, and the Florida record should perhaps be likewise disposed of. (p. 151.)

GRACILARIA BIFLABELLATA J. Ag. This plant is recorded as having been communicated by Mrs. Curtiss, and so is probably from Florida (J. Agardh, Spec. Gen. et Ord. Algarum 3⁴: 87. 1901). The plant, which somewhat suggests *G. lacinulata* in appearance, is by no means well known. (p. 151.)

GRACILARIA DURA (C. Ag.) J. Ag. Since the only report from Florida involving this species apparently is that of Hooper (1850), and since other reports from the American tropics are unsatisfactory, the record may be considered very doubtful. Material originally under this name in the New York Botanical Garden, apparently collected by Wurdemann, seems to belong to *G. cornea*. (p. 154.)

GRACILARIA HELMINTHOCHORTON. This name is assigned to a Florida alga by Hooper (1850), but no other use of it is familiar to the writer. The record may be considered as of no value. (p. 154.)

GRACILARIA TRIDACTYLITES Crn. This plant is attributed 'ad oras insulae Sanctae Augustini (Dā. Hall)' in DeToni (Sylloge Algarum 6: 269). Mrs. Hall's material was primarily from Florida, so St. Augustine in northern Florida is probably the source of her specimens. The plant is by no means well known. (p. 155.)

HYPNEA ROBUSTA. This name is assigned to a Florida alga by Hooper (1850), but no other use of it is familiar to the writer. The record may be considered of no value. (p. 157.)

POLYSIPHONIA FOENICULACEA (Drap.) J. Ag. Murray (1889) records this plant under the name *P. hirta* as having been reported from Florida by Harvey and Melvill. It does not seem to be in Harvey's Nereis (1853, 1858) under either form; lacking other records from tropical America, its occurrence must be considered very doubtful. (p. 183.)

CALLITHAMNION POLYSPERMUM C. Ag. Murray records (1889) this species from Florida on the authority of Harvey

(1853), who considers that it is present at New York, Charleston and St. Augustine. Hoyt (1920) rather hesitatingly records it from Beaufort. As it has not been found to be a member of the southern Cape Cod flora, its occurrence in the north is unconfirmed, and altogether it is best to hold the Florida record in question in the absence of authentic material. (p. 189.)

GRIFFITHSIA CORALLINA (Lightf.) C. Ag. Harvey (1853) records from Florida what is probably *G. globulifera*. The European *G. Corallina* is doubtfully present in the American tropics, although Sluiter (1908) has indeed reported it from Venezuela. (p. 194.)

SPERMOTHAMNION PELLUCIDUM (Farl.) DeToni. Murray (1889) accepts this plant as from Florida under the name of *Callithamnion pellucidum*. Perhaps the record should be held in question until the plant is re-collected and better known. (p. 196.)

CORRECTIONS TO TEXT ON FLORIDA ALGAE

It is appropriate to call attention here to errors which have so far been recognized in the writer's Marine Algae of Florida (1928). It is neither necessary to correct nor significant to indicate in detail the infrequent typographical errors. Omissions have been discussed earlier in the present paper. The following are mistakes which may prove misleading if uncorrected:

Page 44, 51, 191 and elsewhere: references to Farlow (1891) and (1882) read as (1881), and Farlow (1875) as (1876). Page 89: the authorities for the first species described should be *Udotea conglutinata* (Ellis & Solander) Lamouroux. Page 94: the second species described should be spelled *Derbesia vaucheriaeformis* (Harvey) J. Agardh. Page 95: the parenthetic clause in the third line of the description of *Caulerpa Ashmeadii* should read—(pinnules 1 to 2 cm. long). Page 100 and elsewhere for citations of Foerskal read Forskål, but see Collins (1909, p. 413, 419, etc.). Page 102: the correct citation of the second variety mentioned is var. *occidentalis* (J. Agardh) Børgesen. Page 107: line 3 of the comment upon *Ectocarpus confervoides* lacks the word 'Howe' before the initial word 'reports.' Page 121: *Dilophus* should precede *Neurocarpus*. Page 124: the correct citation for the first species described

should be *Spatoglossum Schroederi* (Mertens) J. Agardh. Page 126: the second species described should be cited *Sargassum cymosum* C. Agardh. Page 131: the name at the end of the first line should be C. Agardh. Page 149: *Eucheuma isiforme* is illustrated on Plate 23, fig. 2. Page 169: the correct citation of the first form mentioned is forma *disticha* J. Agardh. Page 186: *Vidalia obtusiloba* is illustrated on Plate 29, fig. 4. Page 189: the name on the first line should be *Callithamnion byssoideum* Arnott.

Page 196: SPYRIDIA. The distinguishing features for *S. aculeata* and *S. filamentosa* seem unsatisfactory as proposed. The Florida variety of *S. aculeata* may be recognized by the hamate tips of the branches and by the recurved spines on the ramular nodes, as well as by habit, since these features are not found in *S. filamentosa*. But the characters offered, based on the number of cells at the nodes of the ramuli and the relative number of nodal and internodal cells on the main axes, are unsafe. It appears that on the ramuli the nodal cells may exceed 8 in both species, though more numerous in *S. aculeata*. On the axes both have at first cells twice as broad and half as many on the nodes as on the internodes, but in *S. aculeata* these divide to a number equal to those over the internodes sooner than in *S. filamentosa*. Later the zonation becomes irregular and obscure in both species. When, as often happens in depauperate dried material, the hamate tips and recurved aculei are absent from plants with the habit of *S. aculeata hypneoides*, it becomes hard to distinguish sharply from *S. filamentosa*.

Page 210: the first variety described should be cited var. *ornatum* Foslie & Howe. Page 216: for the 53rd entry read—*Enteromorpha* Harvey, (*Chrysomenia*), 159.

UNIVERSITY OF PENNSYLVANIA
PHILADELPHIA

Literature cited

(With the exceptions below, papers referred to in this article will be found listed in the writer's earlier Florida algae report, 1928.)

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Aconitum macilentum Greene

WILLIAM A. DAYTON¹

(WITH PLATE 4)

In 1912 Mr. Charles E. Fleming (now head of the Department of range management at the Nevada Agricultural Experiment Station) and Mr. Jesse L. Peterson (now range examiner on the Whitman National Forest) made plant collections, aggregating 225 specimens, in connection with a grazing reconnaissance of the Minam (now part of the Whitman) National Forest, northeastern Oregon. Among these specimens is a monkshood, Mr. Fleming's no. 151, Forest Service serial no. 5171, collected at 6800 ft., in meadows near the base of Eagle Cap, the highest peak in northeastern Oregon. This specimen was pronounced by the late Dr. E. L. Greene (at that time consulting botanical expert of the Forest Service) to be new to science and was named and described² by him as:

Aconitum macilentum Greene, spec. nov.

Radix parva, tuberiformis, ovata, fibras tenues nigrificantes emittens. Caulis unicus tenuis erectus simplex, 3-5 dm altus, foliis paucis breviter petiolatis instructus, apicem versus, una cum florum pedicellis, pilis virentibus molliter hirtellus. Folia utrinque glabra, profunde, subdigitatimque 5-lobata, lobis late lanceolatis, aut subintegris aut incisae dentatis. Flores perpauci, tenuiter pedicellati; sepala anteriora oblongolanceolata; galea elongato, sacco brevi obtuso. rostro subulato, longiusculo, horizontaliter extenso, et cum petalis exterioribus piloso-ciliato.

Minam National Forest. Oregon, 25 Aug. 1912,³ C. E. Fleming. The species, though quite tall, is slender and delicate, the flower in some specimens one only.

It will be noted that Dr. Greene makes no reference to his disposition of this specimen. It was never returned to the Forest Service range plant herbarium in Washington.

Mr. Douglas C. Ingram, in charge of range research in the Portland (Oregon) office of the Forest Service, has recently submitted to Washington for certain editorial matters the District office headquarters duplicate of this specimen, and this has proved to be a true co-type of *Aconitum macilentum* Greene.

¹ In charge range forage investigations, office of Range Research, U. S. Forest Service.

² Greene, Edward L. *Novitates Boreali-Americanae*, VII. Repert. Spec. Nov. 13: 321. 1914.

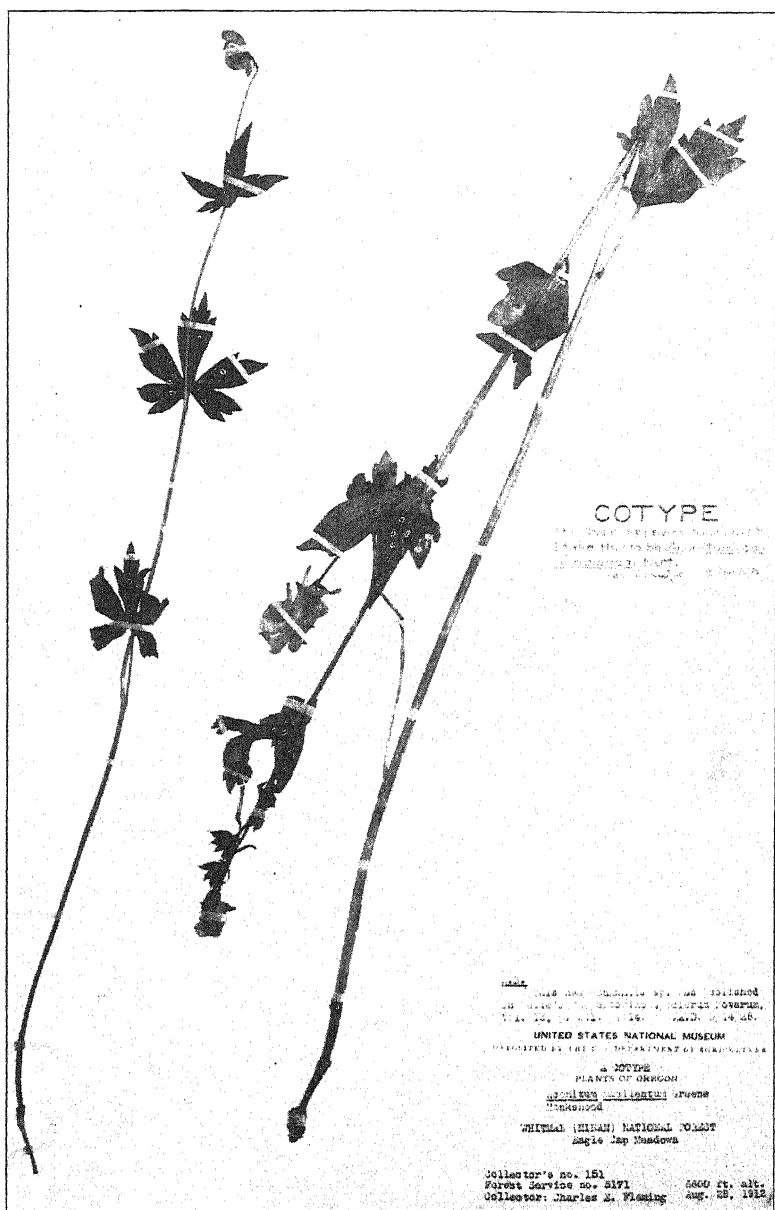
³ Forest Service duplicate material all has 'August 28, 1912,' as the date of collection; '25' is probably a typographical error.

The type of the species appears to be lost—at least it is not in the U. S. National Herbarium. The Forest Service has, therefore, deposited the very satisfactory duplicate from its Portland office, as co-type, in the type collection of the National Herbarium (plate 4).

While this Minam plant is, as Dr. Greene evidently implied in his specific name *macilentum*, rather 'thin' and depauperate, yet this condition might be anticipated by anyone familiar with its somewhat bleak habitat, and I am personally unable to see differences between it and typical *Aconitum columbianum* Nutt., the common monkshood of the Blue Mountains. In fact I saw this monkshood in its type locality the summer before Mr. Fleming collected it, but failed to collect it as I assumed it to be the same as the monkshood elsewhere common in the region, the general form of flower and leaf being individual. Mr. Ivar Tidestrom, to whom the specimen was recently shown, agrees that he cannot distinguish it from *A. columbianum*. Apparently *Aconitum macilentum* Greene must be remanded to synonymy under *A. columbianum* Nutt.

Explanation of plate 4

Co-type of *Aconitum macilentum* Greene, now deposited in the type collection of the United States National Herbarium.



CO-TYPE OF ACONITUM MACILENTUM GREENE

Type of the genus *Jatropha*

KENNETH K. MACKENZIE

The original description of the important tropical genus *Jatropha* L. (Gen. Pl. 288.1737) was as follows:

JATROPHA*. Manihot *Tournef.* 438. *Dill.* elth. 173. *Jussievia*
Houst. A. A. 721.

**Masculini Flores:*

CAL: *Perianthium* vix manifestum.

COR: monopetala. *Tubus* brevissimus. *Limbus* quinquepartitus: *laciniis* subrotundis, concavis, patentibus.

STAM: *Filamenta* decem, subulata, in medio approximata, quinque alterna breviora, erecta, corolla breviora. *Antherae* subrotundae, versatiles.

PIST: *Rudimentum* debile in fundo floris latet.

**Feminini Flores* in eadem umbella cum masculinis.

CAL: ut in masculinis.

COR: ut in masculinis.

PIST: *Germen* subrotundum, trisulcatum. *Styli* tres, dichotomi. *Stigmata* obtusa.

PER: *Capsula* subrotunda, tricocca, trilocularis: *loculis* bivalvibus.

SEM: solitaria, subrotunda.

In the companion volume, *Hortus Cliffortianus* (p. 445. 1737-9) Linnaeus gave three species, as follows:

1. *Jatropha foliis multipartitis laevibus, stipulis setaceis multifidis.* (To this species in 1753 he gave the name *Jatropha multifida*. It is the plant figured by Dillenius and cited by Linnaeus at the commencement of his description of *Jatropha*.)

2. *Jatropha foliis palmatis dentatis retrorsum aculeatis.* (To this species in 1753 Linnaeus gave the name *Jatropha urens*. Both in the *Genera Plantarum* (p. 384) and in the *Hortus Cliffortianus* he drew attention to the peculiarities of this species, but these were not sufficient he thought to constitute a distinct genus. He first thought *Jussievia* Houston was based on this plant and his remarks are made to apply to *Jussievia* of Houston.)

3. *Jatropha foliis cordatis angulatis.* (To this species in 1753 Linnaeus gave the name *Jatropha Curcas*.)

Both species 1 and 3 have sepals and petals well developed, and do not agree with the Linnaean generic description.

In the fifth and sixth editions of the *Genera Plantarum*, Linnaeus described the genus much as in the first edition, but

made some changes. His description in the fifth edition (p. 437. 1754) reads as follows:

961. JATROPHA*. *Manihot Tournef.* 438. *Dill. elth.* 173. *Jussievia Houst.* A.A.

**Masculi Flores.*

CAL. *Perianthium* vix manifestum.

COR. monopetala, hypocrateriformis. *Tubus* brevissimus. *Limbus* quinque-partitus; *laciniis* subrotundis, patentibus, convexis, subtus concavis.

STAM. *Filamenta* decem, subulata, in medio approximata, quinque alterna breviora, erecta, corolla breviora. *Antherae* subrotundae, versatiles.

PIST. *Rudimentum* debile in fundo floris latet.

**Feminei Flores* in eadem umbella cum masculis.

CAL. nullus.

COR. pentapetala, rosacea.

PIST. *Germen* subrotundum, trisulcatum. *Styli* tres, dichotomi. *Stigmata* simplicia.

PER. *Capsula* subrotunda, tricoeca, trilocularis: *loculis* bivalvibus.

SEM. solitaria, subrotunda.

OBS. J. *Urens Stamina novem, erecta, quorum Tria interiora reliquis longiora, quibus (tribus) setae totidem respondent, singulae singulo filamento prope basin insertae.*

In the 6th edition of the *Genera Plantarum* (No. 1084, p. 503.1764) Linnaeus added the following:

Nonnullae species in floribus Masculis habent Calycem quinquefidum & Corollam pentapetalam l. 3.

The species given by Linnaeus in the first edition of the *Species Plantarum* (p. 1006-7.1753) in order were (1) *gossypifolia*, (2) *moluccana*, (3) *Curcas*, (4) *multifida*, (5) *Manihot*, (6) *urens*, (7) *herbacea*. Tournefort's plate 438 cited by Linnaeus in his generic description was not referred to by him in the *Hortus Cliffortianus* (p. 445), nor was it referred to by him in the *Species Plantarum* (p. 1006-7), although the synonymy given by Tournefort (p. 658) was given by him and he based his *Jatropha Manihot* on it.

In the second edition of the *Species Plantarum* (p. 1428-1430.1763) Linnaeus divided these seven species into two groups, the first containing four species which he called the 'calyculati' and the second with three species which he called the 'acalyculati.'

A comparison of the Linnaean generic description with the seven species given by him developed the interesting fact that only one of these species agrees with his generic description.

His description calling for but one well-developed floral envelope was evidently based on the first plate (Tournefort 438) cited by him, to which it entirely applies. When he added his reference to Dillenius he did not modify his generic description to properly include the plant of Dillenius, although the plate cited is of a plant with two floral envelopes very well developed.

In 1763 he definitely noted that his first four species had two floral envelopes, but he never enlarged his generic description to properly embrace these species.

He always appreciated that *Jatropha urens* and the plant of Houston, his last two species, did not entirely accord with his generic description, and he drew attention to this several times.

In other words the original generic description of Linnaeus was based solely on *Jatropha Manihot* L. and it is the only one of his seven species which agrees with his generic description. It in consequence must be taken as the type of the genus.

INDEX TO AMERICAN BOTANICAL LITERATURE

1928-1929

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Morphogenesis in *Polysphondylium*

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(WITH PLATES 5-9)

The problems of morphogenesis are at least becoming more clearly formulated. The new evidence of the effectiveness in plants as well as animals of form and growth determining stimuli transmitted by specific cell products (Went, 1927) puts the conceptions of cellular and tissue interactions on a much more definite basis. With the tendency to recognize the so-called mechanism of heredity as adequately elucidated, it is recognized also that the solution has so far yielded relatively little in the way of data as to the processes by which the chromosomal factors in the egg come to expression and determine the characters of the adult organism. Real progress has been made. In place of the simple factor per character, or the even simpler presence and absence conception, it is now sometimes assumed that all the factors may influence all the characters. This is an advance toward a recognition not only of the real complexity of the problem but also of the facts of correlation, of the interrelation of the parts, in the make-up of the organism as a whole, as contrasted with the conception of organic unity as being nothing more than the chance aggregation of hard and fast unit factors—the *Anlage* of specific unit characters.

The general facts of the life history and method of building the sorocarps of *Polysphondylium* are well known from the studies of Brefeld (1869), Van Tieghem (1880), Olive (1902), and others. I have endeavored by a more detailed study of the activities of the myxamoebae and the pseudoplasmodium to discover the morphogenetic factors involved in their behavior and the building of the mature plant with its differentiation of soma and spore plasm. I have, as with *Dictyostelium* (1926), endeavored to bring out the essential facts in a series of photographs. The quality of these photographs leaves much to be desired. The excuse for this is, again, the inherent difficulty of the material. All the figures of mature plants were made from petri dish dung agar cultures photographed from above, the

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plants having curved over sufficiently to permit getting the low magnification views as shown.

In its structural specialization *Polysphondylium* goes a step farther than *Dictyostelium*. Its sorocarps show secondary lateral elements or branches, as well as the central axial stipe and terminal sorus characteristic of *Dictyostelium*. As in the cormophytes these branches are essentially replicas of the central axis on a smaller scale and with changed tropistic response. The development here, as has been shown for the Boston fern, is one of reduplication of parts (Benedict, 1916), or homoeosis (Bateson, 1894). Another step would naturally be the development of tertiary and further successively subordinated series of branchlets. Such types are known in the Thamnidiaceae and various other groups of fungi and in *Caulerpa* and many other algal forms. Uittien (1929) has recently pointed out that there is correlation in very many cases between the type of venation in the leaf and the type of branching of the inflorescence, a phenomenon which suggests that the physical background underlying such phenomena as homoeosis may also be common to both determinate and indeterminate growth forms.

As in my study of *Dictyostelium*, I shall call the completed plant the sorocarp; its main axis, the stipe or sorophore; the terminal and lateral spore masses, sori. For convenience, without implying morphological equivalence, we may call the points of origin of the whorls of branches nodes, and the segments of stipe between the nodes the internodes; node and internode constitute a phyton (Gaudichaud, 1841). The portion of the stipe between the uppermost whorl of branches and the terminal sorus we may call the terminal segment. The pseudoplasmodial mass after it has left the substratum and is building the stipe and branches we may call the sorogen or sorogenic mass. The form changes by which the myxamoebae fit themselves together in building the stipe with its evenly tapering outlines, dense parenchyma-like structure, and curves developed to maintain its balance, we shall regard as before as involving morphallactic transformations in cell form. The creeping, definitely oriented translocatory movements, by which the myxamoebae move upward to build the stipe and outward to build the branches we may call respectively anallactic and diallactic amoeboid movements.

I shall, for convenience, consider these pseudoplasmodial types in which the mature plant shows a clear differentiation of soma and germ plasm as semi-coenobes. I have elsewhere (1926) discussed the evidence that such forms illustrate at least transition stages between protophytes and metaphytes. For convenience, also, I shall distinguish the processes of cell enlargement by food assimilation and cell multiplication by division as respectively mass growth and census growth. That both morphogenetic and intracellular cell differentiation resulting in organogenesis and histogenesis are phenomena that can advantageously be considered in a special category of life processes, distinct from growth in size, is well shown in the life history and development of *Polysphondylium*.

Structure of the mature plants. Before describing the growth and morphogenetic processes by which the plants are formed, we may note the general facts as to their appearance, symmetry, size-relations, etc. The range of variation in size, number of branches, and general proportions of the plants of *Polysphondylium* is comparable to that in the higher fungi and algae and in the seed plants. This is shown in the figures of plate 5, which are chosen to give an idea of the apparently fluctuating variability of the sorocarps as they develop on dung agar in petri dish cultures. I have so far not attempted to isolate races by selection and propagation of the various types which appear in such populations. The species with which I have worked is apparently *P. violaceum* Bref. My material was obtained from cultures of rabbit dung on garden soil as described by Krzemieniewsky (1927).

As is well known, *Polysphondylium* may produce simple unbranched sorocarps and occasionally *Dictyostelium* is branched. However, the branched colonies of *Dictyostelium* which I have seen are of the type shown in my figures 5 and 6, plate 6 (1926), in which it is possible that the branch was not developed as a segment from an apical sorogenic mass but was formed by a second colony of myxamoebae which crept up the stipe of an already completed sorocarp to a point favorable for the formation of its own plant body and then developed what appears to be a branch. Olive (1902, p. 480) speaks of branches of *Dictyostelium* formed in both ways. Unbranched forms of *Polysphondylium*

(pl. 5, figs. 1, 2) are much more common in my experience than are branched forms of *Dictyostelium*. These unbranched forms may occur in the same petri dish culture mingled with others which have reached the full normal development with eight or ten whorls of branches. They in general are to be regarded as diminutive or slender forms, though well proportioned as to tapering of stipe and size of sorus. The relative number of cells in the stipe is obviously larger than in the case of the plants with many branches. Figure 3 shows a sorocarp with only a single lateral branch which was apparently formed from a segment of the terminal mass though its development was not seen. Its size both as to length of stipe and diameter of sorus suggests that it represents perhaps the simplest possible expression of the tendency to form whorls of branches on the main axis. The diameter of the lateral sorus as compared with the terminal sorus is a little large, about 1:1.6, instead of the general average of about 1:2. The entire height of this sorocarp is not shown, as the base of the stipe was hidden by the substratum. I have occasionally seen sorocarps with a single lateral sorus having a very short stipe or no stipe. Such a case is shown in figure 4. In figure 1, there is also a small lump about half way up the stipe which may be a mass of slime or may contain amoebae.

Figure 5 shows a sorocarp with a single whorl of three branches, and perhaps more normal proportions, though here again the full length of the stipe is not shown. The average diameter of the lateral sori compared with that of the terminal sorus is about 1 to 2. The relative length of the terminal segment of the stipe to that of the branches is of the same general order here as in the more branched sorocarps shown in figures 8, 9, and 14, 15, 16.

The branched sorocarp in figure 6 shows a form with the terminal segment unusually short, giving the plant a stunted appearance as compared with the more common forms. Such types are quite unusual. Figure 6 shows also a simple unbranched sorocarp (6b) arising from nearly the same region of the substratum from which the branched sorocarp (6a) arises. This close association of sorocarps is not uncommon in my cultures, and frequently at least the unbranched sorocarp is formed later. Figure 7 shows

a plant with two nodes, the upper one with a single branch, the lower one with three branches. Figure 8 shows another plant with two whorls, the lower with three and the upper with two branches. The internode is relatively short and the terminal segment much longer than the internode, and the latter is also relatively much longer than the terminal segments in plants 7 and 10. Figure 9 shows a plant with two whorls of four branches each, the relative lengths of the internode and the terminal segment being more nearly normal. Figure 10 shows a rather normally proportioned plant with two whorls of branches, four branches at the lower node and three at the upper.

The plant shown in figure 11 has a fairly symmetrical development, with the number of branches in the whorls counting from below 3, 3, 4, 4, 1. The apical and basal whorls show fewer branches than those in the midregion. On the other hand, figure 13 shows a plant with an irregular distribution of branches, the numbers being, counting from below, 3, 1, 2, 4, 4, 4, 4, 3. Figure 12 shows a plant with unusually numerous branches in the lower whorls. The series of whorls of branches shows 2, 1, 6, 6, 5, 5, 5, 4. The average number of branches per whorl for this plant is 4.25, against 3.1+ for all the plants shown on plate 5. The whorl of branches at the third node from the base is strangely one-sided instead of radial, five branches extending more or less to the right of the stipe and only one to the left. Variation in the length of the branches and the size of the sori they bear is conspicuous. The fourth and fifth nodes from the base each have one branch very much shorter than any of the others, and they bear correspondingly diminutive sori.

The plant shown in figure 14 is quite symmetrical in its form. It has two branches in the basal whorl and one in the apical whorl, with five median whorls of three branches each. Figure 15 has an unusual combination, with its lower three whorls showing two branches each and its upper four whorls with three branches each. Figure 16 shows the plant with the largest number of whorls in a single series which we have yet photographed. It has eleven whorls of branches, with the number of branches per whorl from the base up 4, 4, 3, 4, 3, 3, 2, 2, 4, 3, 3.

The range and general character of the variations in such a series of semicoenobitic plants as noted above is in general quite

comparable to the diversity in form and general proportions in higher plant types and in view of the nature of the morphogenetic processes by which these forms are produced this similarity in end results is notable. We have small plants of relatively normal (fig. 10) and stunted (fig. 6a) habit. We have average sized plants with a tendency to regularity in form and the numerical distribution of their parts (fig. 11) and others with notable irregularities in these particulars (figs. 13 and 16). The difficulties in getting the plants properly placed for photographing make it difficult to bring out adequately these facts as to their general habit.

TABLE 1
*Relative dimensions of the parts as shown in a series of
twenty-eight plants*

Ratio of average height to first whorl of branches to average total height	1: 2
Ratio of average length of terminal segments to average total height	1: 3.8
Ratio of average length of internodes to average total height	1: 5.3
Ratio of average diameter of terminal sori to average length of terminal segments	1: 4.5
Ratio of average diameter of lateral sori to average length of branches	1: 2.5
Ratio of average diameter of lateral sori to average diameter of terminal sori	1: 1.9
Ratio of average diameter of terminal sori to average total height of branched plants	1: 17.1
<i>Plants with no branches</i>	
Ratio of average diameter of terminal sori to average height of plants	1: 10
Ratio of average height of unbranched plants to that of branched plants	1: 2.6
Ratio of average diameter of terminal sori of unbranched plants to that of branched plants	1: 1.6

The percentage distribution of cells to soma and germ tract tends, more or less, to be preserved whether the colony is large or small. This is all the more remarkable since the determination is apparently achieved at the time when the base of the stipe is being formed. It seems likely, however, that in the long run the relative number of amoebae massed together at the time the

stipe base is started is a fair index of the number that will probably be present in the later stages of differentiation of the sorocarp.

The most constant dimensional elements are the distances between the whorls of branches, the relative length of the branches in successive whorls, the distance between the last whorl of branches and the terminal sorus, and the relative diameters of the lateral and terminal sori. The terminal sorus is always larger than any one of those on the lateral branches. The sori on the branches of a whorl vary in size with the length of the branch which bears them. Certain of these dimensional relations as measured with the horizontal microscope on 28 sorocarps grown in small test tubes are given in table 1.

There is perhaps a tendency to form fewer branches in the basal and apical whorls, though this by no means always comes to expression. Six plants shown in plate 5 (fig. 7, 8, 11, 12, 13, 14) have fewer branches on the terminal node than on the one next below. In sixteen plants from a single culture, whose number of whorls varied from three to eleven, the average number of branches on the basal node was 2.5+, on the distal node was 2.8+, while the average for the remaining nodes was 3.6. The larger sorocarps may have as many as fifteen whorls of branches.

Free swarming and aggregation stages. The myxamoebae may be quite different in appearance at successive stages in their development. Figure 17 shows them moving rather sluggishly in a hanging drop dung agar culture, and tending to remain about isodiametric in their general outlines. In figure 18 they appear more slender and elongated and are creeping about somewhat more actively, though not showing any evidence of a concerted movement in a specific direction.

I have worked for the most part with richly nourished cultures of *Polysphondylium*, in which the amoebae become very numerous within the first twenty-four hours. In such cultures when they come to maturity the myxamoebae very soon form thick dense strands converging on the site of the future sorocarp. In such streaming strands the movements of the individual myxamoebae cannot be followed. Rivers of myxamoebae extend frequently for long distances across the culture medium. In petri dish dung agar cultures of *Polysphondylium* I have ob-

served no tendency to the choice of any specific type of loci for the formation of the sorocarps. In my hanging drop cultures of *Dictyostelium* the sorocarps were quite commonly formed at the edge of the culture liquid. When the surface of the medium is scratched and a furrow made by the inoculating needle many of the first formed sorocarps of *Polysphondylium* are in or near this roughened region. This makes difficult the microscopic study and photographing of the base of the stipe in such cases. In well-developed cultures, however, the sorocarps are rather evenly distributed throughout the area of the petri dish. There is no evidence of the formation of concentric zones of sorocarps. Their development from day to day is in quite irregular and patchy groups.

In the case of *Dictyostelium* my cultures were made and figures of the aggregation stages chosen to illustrate the behavior of the free amoebae as they collect to form the sorocarpic mass (1926, plate 7, figs. 17-22). Such stages were relatively neglected by the earlier workers. For *Polysphondylium* I have photographed the more massive pseudoplasmodia as they flow together to start sorocarp formation. My observations confirm in general the data given by Brefeld (1884) and Olive (1902). Stages in the process of aggregation to form sorocarps are shown in figures 19, 20, and 21.

Figure 19 shows the central portion of a rather symmetrical radially well-developed pseudoplasmodium in which the young sorocarp is merely a central mass toward which the radiating streams of myxamoebae are creeping. There are about ten main elements in this converging system. Each of these is made up by confluence of smaller streams. The larger of these strands meet as a rule at angles of less than 45° . There are, however, especially toward the center, many smaller laterals which may enter the main streams at angles of 60° to 80° . Anastomoses between the smaller branches are not uncommon.

Figure 20 shows the central mass developed further into an upwardly extending conical or cylindrical column. The end of the cylinder is enough out of vertical so as to appear in the photograph, taken from above, as a dark, short, finger-like stub projecting upward in the figure. About ten main converging streams are shown in this figure. The confluence of smaller

streams to make these larger pseudoplasmodial elements is shown as in figure 19. The fringe-like, smaller streams coming into the large streams at wider angles are not so much in evidence. The main streams hence appear more clean-cut. As only the central region of the system is included in the figure, the peripheral shortening of these main streams as a result of the centripetal flowage is not shown. Figure 21 shows the same pseudoplasmodium which is shown in figure 20, more highly magnified and a few minutes later. Various minor differences in the smaller branches can be made out, though the general configuration is unchanged.

Figure 22¹ shows a young sorocarp further advanced in its development, but with the outlines of the pseudoplasmodium which formed it still plainly shown on the substratum. The young sorocarp forms a somewhat S-shaped curve, and is sufficiently out of the vertical to make possible the photograph as shown, looking down on the culture from above.

The whole system of pseudoplasmodial branches in this case, as happens many times, was quite one-sided. The streams of myxamoebae formed a watershed-like system of many stream lines, thinning out and branching repeatedly toward their extremities. As noted, the streams of myxamoebae leave paths or furrows in the agar medium which persist after all the amoebae have reached the central mass. At the magnification used in these particular figures it is not always easy to be sure in the photograph whether a given converging element in such a system is made up of the streaming amoebae themselves or is merely the track they left in the agar. In either case the orientation of the converging streams is correctly indicated. In the present case (fig. 22) the pseudoplasmodial outlines, for the most part, at least, merely mark the paths made by the streams in the agar; while the pseudoplasmodial mass itself has now become largely, if not wholly, the young slightly S-shaped sorocarp. The nature

¹ This particular figure is confused by the presence of the lower portion of the stipe of another completed sorocarp which has its base a little above and to the right of the one which is being formed. This segment of stipe appears as the thick, black line curving in a wavy direction downward to the base of the figure and gradually going out of focus. It has no relation to the sorocarp under consideration.

of the morphogenetic process as one of cell translocation and not of growth is thus sharply visualized. The branching slimy furrows which the streaming mass left behind persist for some time in the substratum. The pseudoplasmodial mass of cells has transformed itself by specifically oriented synallactic creeping movements into the more or less erect columnar young sorocarp. From the standpoint of the stimuli involved there is here exhibited a sort of centrotropy whose expression may be compared to the *Suchbewegungen* of the elements of the higher plants, as Janse has recently distinguished them (1927). The obvious distinction to be recognized is that the movements of tendrils, twining stems, growing points, etc., involve no extensive changes in the spatial interrelations of the cells of which the moving parts are composed. The advance of a root tip is due to the specifically oriented enlargement of the daughter cells and their division, when mature, in specially determined planes. It is a matter of growth movement; but the distinction between such oriented growth movements and creeping movements is largely one of degree. The wanderings of the free amoebae on the substratum in their growing stages (figs. 17 and 18) necessitate extensive creeping, specifically oriented translocations, in order to bring them into the mutually compacted relations which the root cells never lose. That in both cases the movement is the expression of the oriented activities of the individual cells as such is obvious in the light of the phenomena in *Polysphondylium*. The stimuli which determine this centripetal migration, while difficult to determine specifically, are clearly not from the physical environment in even the degree suggested for *Dictyostelium*, in which the locus for a sorocarp and the direction of flowage are frequently at least, as noted, toward the drier margins of the culture medium. The stimuli are obviously attractions for each other existing between the amoebae and are in some degree at least proportional to the mass of amoebae in any given direction from the moving stream. The reactions to the stimuli are in their expression centrotropic.

That the individual amoebae are able to trail each other by chemical stimuli or physical stimuli from slime, etc., even when not in contact, is clearly suggested in my photographs of the aggregation phases in *Dictyostelium*. There is probably no reason

for assuming the existence of any other factors of stimulation in the case of the pseudoplasmodial flowage shown in figures 19-22. Much less is there any reason for assuming any super-chemical or physical stimuli or the action of organizing or regulating principles associated with the multicellular organismal conditions resulting from the aggregation of the myxamoebae. The behavior of the pseudoplasmodium as a whole is the sum of the behaviors and reactions of the individual myxamoebae.

Stipe and branch formation. In my cultures the pseudoplasmodium commonly frees itself from the substratum rather early and proceeds upward as a cylindrical mass, building the sorophore to quite a height before branch formation begins. In other cases, as seems more common in *Dictyostelium*, this terminal mass remains connected for some time by a long strand or river of amoebae flowing up the newly formed stipe and extending below into the similar streams of amoebae creeping toward the base of the forming sorocarp. In typical cases before branch formation begins the whole mass of myxamoebae is aggregated in a terminal cylinder, the sorogen, at the apex of the forming stipe.

The stages at which the sorogenic mass is just freeing itself from the substratum are naturally very difficult to photograph in petri dish cultures, since the young plants rarely bend over sufficiently to give a side view from above the culture. Figure 23 shows a stage in which the stipe has reached a length about twice that of the apical sorogen which is building it. In this case there is no stream of amoebae at this stage connecting the sorogen with the substratum.

The sorogen is cylindrical, narrowed toward its base, and almost papillate at its apex, as is well shown for a later stage in figures 25 and 26. This is typical for *Polysphondylium*, and the further development of the sorocarp consists in the elongation of the stipe and the metamorphosis of the apical mass into the whorls of branches and the apical sorus. The length of the stipe, before branching begins, varies greatly and is probably more or less influenced by environmental conditions. It is difficult to get exact measurements of its length in petri dish cultures, but as noted above, measurements of 28 plants with the horizontal microscope indicate that the height of the stipe to the first whorl of branches is about one half of the total height.

The process of building the branches consists in the beginning in abstricting a thick, ring-like, cluster of myxamoebae from the base of the sorogen. Figure 24 shows such a mass already left some distance behind by the further advance of the sorogen. Such ring-shaped clusters I shall call, for convenience, segmental masses. They are successively produced in metameric order until all the whorls of branches are provided for. As many as six such masses may be cut off before the first has completed its differentiation into a whorl of branches (fig. 34).

The first indication of the cutting off of a segmental mass is the appearance of a rather broad constriction toward the base of the sorogen. This is well shown in figure 26, which represents a young sorocarp with three segments cut off and left behind in serial order and the fourth just forming. The abstriction of such a segmental mass suggests cleavage of the cellular aggregate into two unequal parts—the larger part continuing to build the stipe upward, while the smaller remains behind to form the whorl of branches. The broad constriction formed does not, however, suggest the sharp cleavage furrows found in the cutting up of the aethalium of a slime mold or the sporangia of the Mucorineae into spores. It seems more probable that what is taking place here is a sort of catenoidal break-up of the viscous colloidal sorogen, due to the successive lagging behind of masses of myxamoebae at its basal end. The myxamoebae at the apex of the stipe continue to build it higher. Those at the basal end successively reach a stage at which they cease to advance and the two groups separate as a result of the pull from above, with the more rigid stipe affording a support to which the passive basal mass is left adhering. Such serially disposed segments as are shown in figures 25, 33, and 34, suggest the catenoidal series of droplets into which a somewhat viscous thread will break up when submitted to longitudinal strain. The obvious difference here is that the stipe remains as a string on which the catenoidal beads are strung. Two successive stages in the process of constriction are shown in figures 25 and 26. In figure 25 the narrowing is barely visible but a little later, as shown in figure 26, the broad shallow furrow is well marked. The proximal slope of the furrow tends to be ridged, indicating that the myxamoebae of the segmental ring are already beginning to draw to-

gether and form a more rounded mass. The segmental mass when first cut off is typically spindle- (fig. 24) or top-shaped (figs. 25 and 26, the upper segment), but the amoebae immediately tend to draw together, reducing its surface of contact with the stipe. Very soon projections appear on the surface of the segmental masses, indicating the beginning of branch formation, and if successively older segments are compared the stages in the process may be followed on the same sorocarp (figs. 32 and 34).

It happens very frequently, as a result of the changes and disturbance incident to photographing, that the young sorocarps lop over so far that the sorogen comes in contact with the substratum. This situation leads at once to a very specific autoregulative reaction. The myxamoebae of the sorogenic mass at the point of contact with the substratum turn about and begin to once more build the stipe more or less vertically upward from the new point of support as they did from the initial point at the beginning of sorocarp formation. If the disturbing condition is recurrent this process may be repeated, resulting in a sort of successive looping down of the stipe resembling the stoloniferous growth of the common breadmold, *Rhizopus stolonifer*.

This characteristic morphogenetic reaction does not, however, prevent the normal process of sorus-formation. If branching has not begun it is delayed until anallactic migration in the new direction has carried the sorogen to the necessary distance from the substratum, when it begins to form the segmental masses and continues development until the sorocarp is complete or the process is interrupted by a repetition of the toppling over and contact with the substratum. If branching is already under way when the whole plant bends over a most characteristic situation develops, illustrating with the greatest clearness how an aggregate of free individual cells on the emergence of a new situation can alter their behavior to meet the new conditions with all the definiteness of the most highly integrated systems of tissues and organs. The new set of, in this case, spatial interrelations induces the substitution of a new specifically different set of reactions in the system; and this happens in a system of elements the cell units of which are entirely equivalent and totipotent both in their visible appearance and their reaction potentialities. Such possibilities in behavior we have been inclined to assume imply a

high degree of visible integration, and constitute one of the main supports of organismal hypotheses and the assumption of integrating principles. The series of stages in the development of a single sorocarp, which are shown in figures 27 to 31, illustrate such a situation. The pictures were taken at intervals of from ten to twenty minutes. In the stage shown in figure 27 three segmental masses have been formed. The sorogen, which has been developing soma (stipe) at its apex and abstricting segmental masses at its base in a definite rhythm, now intermits completely the latter process while continuing the former. The cellular morphallactic form adjustments, by which the smoothly tapering stipe was being formed and at the same time its balance maintained and its elongation directed away from the substratum, suddenly swing the axis of elongation of the stipe through an angle of upwards of 90° and thus tend to regain the orientation vertical to the substratum. It is to be noted that this is accomplished equally well in either erect or inverted (hanging drop) cultures. The bend in the stipe is smoothly rounded, showing the utmost nicety of adjustment between the molding cellular interactions by which the tapering form of the stipe is maintained and the cellular response to changed environment by which the new direction of elongation is achieved. The whole procedure simulates in all superficial features a growth curvature and yet there is no growth in number of cells or mass of assimilated materials. The whole process is one of coördinated creeping, anallactic movements, anaphytosis (Schultz-Schultzenstein, 1861), of individual cells and morphallactic changes in their form as they fit themselves together to build the stipe. All three segments are still in the early stages of development as merely thick, massive, ring-shaped groups of myxamoebae encircling the stipe. Meanwhile, the whole plant has lopped over. The sorogen has come in contact with the substratum and has at once begun to bend up in a new direction of anallactic migration by the amoebae. In figure 28 the new axis of advance is well fixed and the sorogen is smoothing out into its normal form. The region of contact of the sorogen with the substratum is conspicuously marked by an oblong depression in the agar medium filled with slime and with a rounded thickened mass at the end from which the stipe extends upward. In figure 29 the sorogen is still nearer the ver-

tical and has raised itself from the new point of departure by a stipe which is about one-fourth its own length. In figure 30 the new segment of stipe is about the length of the sorogen, and in figure 31, fifteen minutes later, it is a little longer than the sorogen.

In this series of stages the myxamoebae of the sorogen have thus carried out a characteristic and highly adaptive tropistic response by which, after having toppled over and come in contact with the substratum, they have attained a new foothold, turned upward and in large part regained their normal direction of migration under the influence of geotropic and hygrotopic stimuli. If we turn now to the behavior of the myxamoebae in the three earlier formed segmental masses, we find an equally specific situation. While the amoebae of the sorogen have changed their behavior under the changed conditions, the amoebae of the segmental masses proceed with their morphogenetic processes quite uninfluenced by the new space relations of the system taken as a whole. They have proceeded with the same radially oriented movements as if there had been no change in the orientation of the stipe on which they are borne; that is, they have formed branches radiating from their position on the stipe as a center. The orientation of their migratory movement with reference to the stipe is unchanged, though it is now widely different in respect to the substratum and other environmental surroundings than it would have been if the plant had not bent over. The sorogen has shown itself specifically plastic in the determination of its reaction in accordance with its position in its external environment. The segmental masses made of amoebae, differing from those in the sorogen only by position in the system, show themselves specifically fixed in their morphogenetic reactions regardless of changes in position with relation to the external environment. Such reaction complexes are of course common enough in other plants and have their interest here from the fact of their being so conspicuously matters of cell behavior even though the cells are aggregated in specifically organized colonies.

The process of leaving behind such segmental masses is rhythmically repeated until the mass of the sorogen is reduced to about the volume necessary to make a single segmental mass. When this stage is reached the stipe is built on further to some-

thing more than one and one-third times the length of an ordinary internode (table 1) and the remaining group of myxamoebae rounds up to form the terminal sorus. The lengths of the successive internodes tend to be about equal for sorocarps under constant conditions but wide divergences from type are found in petri dish cultures which are subjected to the disturbances of study and photographing.

The formation of a whorl of branches involves first the localization in the segmental mass of centers for lateral stipe formation. These are more or less symmetrically placed about the stipe, and as noted above vary in number from one to five or even six. The segmental mass is too dense to permit direct observation of the first aggregation of myxamoebae to form the basal groups of these stipe laterals. The important fact morphogenetically is that the amoebae have in erect cultures changed their tropistic reactions so that they creep out radially from the stipe. With relation to their earlier orientation they have become plagiotropic. The sorogenic mass from which they have separated continues negatively hygro- and geotropic and builds the vertical stipe still higher. The segmental mass at first draws together but almost at once begins to build radially placed lateral stipes. The process in its response relations is the same as in the case of any radial and metameric system of branches in the higher plants.

The branches appear first as projections of the segmental mass. If three branches are to be formed it becomes triangular in outline; if the whorl is to consist of four branches the segmental mass becomes four-cornered as viewed from above. The number of branches to be formed is at once indicated by the plastic change in form of the mass of myxamoebae as shown in figures 28, 32 and 34. The side view is not favorable for bringing out these forms in photographs but illustrations of two, three, and four lobed forms can be recognized without difficulty in the figures. That these form changes in the segmental masses are really determined by the formation of the lateral stipes in their interior is obvious from the shapes assumed. Each young branch rudiment is a blunt but tapering papilla rather than an oval swelling. The extension of the slender solid stipe within the plastic mass determines the shape of the projection of which it is the support-

ing axis. The stipe is built on in advance of the movement of the great mass of the myxamoebae. Its elongation is determined by the morphallactic form adjustments achieved by the myxamoebae at its apex. A little later the segmental, ring-like mass of myxamoebae in the upper whorl of the sorocarp shown in figure 29 is seen to have been thus transformed into three oblong cylindrical finger-like projections diverging from the stipe as a center.

Very soon, as in the lower two whorls in figure 29 and in all three whorls in figure 30, the lateral stipes become exposed in their proximal portions and the myxamoebae form lateral sorogenic masses which rapidly push their diallactic migrations to completion and form rounded sori. The segmental masses shown at the three nodes in figure 28 are destined to produce respectively two, one, and three branches, and this is already indicated in their form as shown in the figure. As the lateral sorogenic masses push away from the central stipe, considerable masses of slime are left as anchorage for the branches on the central stipe. The outlines of these slime masses are surface tension curves determined by the viscosity of the slime and its adhesion to the central stipe and the bases of the lateral stipes, as shown in figure 6, plate 6, in my former paper (1926).

The process by which any one branch of a whorl forms itself from a portion of the segmental mass is the same in principle as that by which the central stipe or axis is formed from the pseudoplasmodium. The branch is a lateral element attached by slime to the main axis just as the main axis is attached to the substratum by slime. As Brefeld's and Olive's figures show, there is no tissue connection between branch and stipe such as is found in the branching of algae and fungi generally. In this respect the conditions suggest an analogy with the false branching in the blue-green algae, especially those in which the base of the branch is a heterocyst and hence in some cases somewhat enlarged and rounded.

I have described in some detail and given measurements showing the rate of tapering of the stipes in *Dictyostelium*. The facts there brought out hold essentially for *Polysphondylium*, with one exception. I have noted that in *Dictyostelium* we can distinguish three regions of the stipe as to their rate of tapering:

first, the basal region in which the diameter diminishes very rapidly; second, the median trunk region in which the tapering is very slight, one unit in diameter to 112 units in length; third, the terminal region in which the tapering is again more rapid, 1 to 67. In *Polysphondylium* the median region with a quite inconspicuous rate of tapering is relatively much longer. In the apical region the tapering is again more rapid. The base of a stipe, which in this case is quite irregular and is curved to one side, is shown in figure 35. The normal form is knob-like, or bulbous. The slime mass which anchors it to the substratum is well shown. Figure 36 shows a segment of the stipe of the same plant from the median region where, for long distances, the tapering is very slight. The cellular structure corresponds entirely with that in *Dictyostelium*.

In the extreme apical region within the sorus the tapering may become irregular and there may be a slight thickening, the cells becoming disk-shaped instead of vertically elongated as they are a little further back. This is well shown in figure 37. The morphallactic form adjustments of the cells are obviously less perfectly worked out as the process of building the stipe upward comes to a close, under the influence of the limiting factors resulting from the difficulty in maintaining the cell adjustments called for by the growing height and unsteadiness of the whole sorocarp system. A similar tendency to a failure of the morphallactic cellular responses at the apex of the stipe is seen in *Dictyostelium* (1926, pl. 8, fig. 31) but hardly to the degree that it is in evidence in *Polysphondylium*.

The form of the lateral stipes and their relations to each other and to the main axis can be seen in flattened out water mounts of the sorocarps. As noted, they are in the general method of their formation miniature replicas of the main stipe. The stipes of the branches taper much more rapidly than does the main axis, so that they may be quite club-shaped, as shown in figures 38 and 39. In these two figures, and in figure 41, the base of the branch is thicker than the main stipe at that point. In these water mounts the anchoring slime around the bases of the branches shows not at all or very faintly. The change in form of the cells, from isodiametric polyhedra at the base of the branch to flattened disks in the middle, and more or less elongated

cylinders toward the apex of these larger branches, is a very striking exhibition of adaptive morphogenetic determination, (figs. 38, 41, 43 and 44).

The apical load carried by the lateral stipe diminishes progressively as the cells of the sorogen metamorphose themselves into cells of the stipe and presumably lose weight by drying and destructive metabolism. The stipe must of course carry its own weight as well as the weight of the sorus and considered as a static system the bending moment decreases from its base to its apex.

In the basal portions of these branch stipes, formed while the lateral sorogen is still supported largely by direct adhesion to the main stipe, the outlines tend possibly to be more irregular and the taper less even, as is seen in figures 38, 39 and 41. The variations in size of the branches, both as to length, diameter at base, and rate of tapering, are well shown in figures 38-44. There is no doubt a correlation of these stipe dimensions with the size of the lateral sori. As I have noted, the ratio of diameter of sori to length of supporting stipe is 1:2.5 for the lateral branches, and 1:4.5 for the terminal segment and its sorus. Branches may be not more than one cell in diameter from base to apex (figs. 44 and 45) and in such cases the cells change from thin flattened disks (in some cases twice as wide as high) to isodiametric segments of cylinders and, towards the apex, to forms two or three times as long as they are wide (fig. 44.) I have given data as to the changing relations of width and length of the cells in the stipes of *Dictyostelium* (1926, p. 253). The morphallactic adjustments by which these changes in the rate of tapering are brought about are much more accentuated in the branches of *Polysphondylium*, which taper so much more rapidly. The end cell or cells which are enclosed within the sorus, as in the case of the terminal sorus, may be in some cases less tapering or even somewhat thickened.

The rate of taper in the stipes with strongly bulbous bases, such as are shown in figures 38 and 39, varies more rapidly in the basal region and is much more even in the region beyond the first quarter of the total length. If we divide the whole length of such a lateral stipe into segments, beginning at the base, the variations in the rate of taper in the successive segments can be

measured with such accuracy as the lines in the photograph permit. I have taken for the first segment the distance from the base of the lateral stipe to the point at which it attains its greatest width. The increase in width is relatively very rapid in this region. Beginning at this level of greatest width, I have divided the remainder of the stipe into segments of about equal length and determined the diminution in width for each. Table 2 shows the rate of tapering in a branch with strongly bulbous base, like those in figures 38 and 39, and the corresponding rate in a more slender branch with no markedly bulbous swelling at the base (figs. 43 and 44).

TABLE 2

Rate of taper in two lateral stipes differing in the degree of development of the basal bulb

A. WITH WELL DEVELOPED BASAL BULB			B. WITH THE BASAL REGION ONLY SLIGHTLY BULBOUS		
Segment	Rate of taper		Segment	Rate of taper	
1	Increase	1: $6\frac{1}{4}$	1	Increase	1: 1
2	Decrease	1: $2\frac{3}{4}$	2	Decrease	1: $6\frac{2}{3}$
3	"	1: 10	3	"	1: 20
4	"	1: 20	4	"	1: 40
5	"	1: 100	5	"	1: 40
6	"	0	6	"	1: 40
7	"	0	7	"	1: 40
8	"	1: 40			
9	Increase	1: 40			

As shown for lateral stipe *A*, the rate of taper changes rapidly in the bulbous region, segments one and two. It then narrows less rapidly, segments three, four, and five. In segments six and seven there is no measurable taper. In the ninth segment there is a slight increase in the diameter of the stipe.

As noted in many of the lateral stipes the basal bulb is by no means so strongly developed. In the particular case *B* shown in the table, the rate of taper is practically unchanged from segment four to the apex.

The unit bending stress on a branch diminishes from its base to its apex and its tapering form is an expression of the principle of economy in nature. The diallactic creeping movements of the amoebae in the lateral sorogen and the morphallactic form adjustments by which the lateral stipe is built are all carried out in

progressive order under the influence of the graded differences in bending stress in such a system. The fact that the material for the elongation of the stipe comes from the sorogen, so that the whole system is developed progressively with a continuous change in the relative weight of stipe and sorogen, affords another graded series of changes in the barotropic relations at the focus of morphogenetic activity which may well be assumed to have form determining significance.

Organic regulations. *Polysphondylium*, like *Dictyostelium*, is favorable material for the study of the processes by which teased up fragments of the pseudoplasmodium build new sorocarps. The process in its essential features is simply one of reorganization or reconstruction, with no regeneration of or substitution for lost parts or repair of injury (reparation). Van Tieghem (1880) reported that when a young plant of *Polysphondylium* is teased or crushed out the amoebae separate and renew their vegetative growth and cell division. Later on they begin sorocarp formation anew.

Olive (1902, p. 471) has described the formation of several fructifications from a single pseudoplasmodium when transferred to a fresh drop of nutrient solution. He does not, however, agree with Van Tieghem that in doing this the myxamoebae pass through a further stage of vegetative growth and reproduction. This disagreement may be due to differences in the age of the sorocarps which were used in the experiments.

The process by which a fragment of a pseudoplasmodium builds a symmetrical new sorocarp is that of specifically oriented creeping movements, ordered translocations of the amoebae, and the molding of the individual amoebae together to form the stipe (soma) and the sori (germ plasm) of a new sorocarp. The stages in the transformation of such a mass of amoebae as one of those shown in figure 55 into the sorocarp shown in figure 57 is strictly a matter of morphogenesis and resulting differentiation without either mass or census growth. Nothing is repaired, nothing is replaced by substitution, nothing is regenerated in any sense implying growth. We thus have before us the processes of morphogenesis and differentiation *per se*. The group of myxamoebae simply starts again as a pseudoplasmodium to form a new sorocarp. In such a new plant, as Van Tieghem emphasized

(1880), there is no reason to suppose that any particular cell reaches a position in the new sorocarp corresponding to that it would have achieved if not disturbed. Young sorocarps with a considerable length of stipe are favorable material for studying these reconstructive powers of the myxamoebae. If such young plants are teased up with needles in a drop of water or dung decoction the fragments begin at once the reconstructive processes. For the case just noted figure 55 shows the appearance of two such small masses of myxamoebae photographed in a hanging drop culture at 10 P.M. (magnification 13). They are irregular in outline and many free myxamoebae are regularly present about such masses though not shown at this magnification. Figure 56 shows the same two masses one hour later, 11 P.M. They have moved together and rounded up somewhat. Twelve and one-half hours later, the next forenoon at about 11:30 A.M., they had each formed sorocarps with branches. The upper one shows a stipe with a whorl of branches midway in its height and a single branch or a more or less distinct simple sorocarp at its base (fig. 57). The lower one of the two was not favorably placed for photographing. It showed a sorocarp with one branch near its base and three other branches or independent sorocarps whose relations to the basal mass were not clear. As noted, free myxamoebae were also present in the culture though not visible with the magnification used in making the photographs.

Figure 52 shows a fragment of a stipe with masses of myxamoebae adhering to it as they appeared in a preparation of a young sorocarp teased up in a hanging drop. The photograph was made at 9 P.M. The preparation was photographed again at 10:15 P.M. and showed the myxamoebae rounded up in three main masses along the stipe (fig. 53). The next morning at 11:30 these masses had formed sorocarps as shown in figure 54: at least eight sori are shown with their stipes extending at various angles from the basal masses. When such small sorocarps stand vertically to the plane of the picture the stipe is hidden by the sorus. The basal residual masses consisting of gelatinous material in which the base of the stipe is embedded are quite rounded, and in some cases appear in the photographs to be nearly as large as the sori. They are less dense, however, and more irregular in outline.

Figure 58 shows another longer portion of a stipe and sorogen which was dragged about in a hanging drop of dung decoction and finally mounted. The myxamoebae are distributed in irregular clumps and masses on the stipe, and are already showing a tendency to form rounded groups. Other masses of amoebae were scattered here and there in the culture and the next morning, twelve hours later, many of them had formed sorocarps and were photographed. The largest clump had made at least six sorocarps, as shown in figure 59. Another clump (fig. 60) had made a single sorocarp with a pair of branches about midway of the stipe. Three others were simple and unbranched and of very unusual proportions, the stripes being in length only two or three times the diameter of the sorus. Figure 61 shows a very diminutive specimen with a pair of apparently abortive branches near the base of the main stipe.

Perhaps the simplest case of these morphogenetic regulations is seen when a young sorocarp is bent over until the sorogen touches the substratum. This happens frequently, and I have described such a case above as it occurred naturally in the development of a sorocarp in a petri dish culture. The results of such an interruption of normal development may be studied and photographed under controlled conditions if a young sorocarp, before branch formation has begun, is picked off the substratum and its tip carefully brought in contact with the agar medium in a fresh hanging drop. The sorogen adheres to the agar, and if left in this position with a minimum of disturbance, proceeds almost at once, with no tendency to preliminary rounding up, to the completion of a sorocarp. The stages in this process are shown in the photographs 46 to 51. These were taken from the same preparation at successive intervals of about fifteen minutes. Figure 46 shows the sorogen and a bit of the stipe of a young sorocarp as it has just been picked up, laid in a drop of water and placed in a moist chamber. A certain number of amoebae escape from such a mass, especially at its apex, but in general they do not appear clearly in the photograph. The trumpet-formed widening of the stipe at its extending apex is shown here as in my figure 14, plate 6 (1926) of *Dictyostelium*. The diagonal line running past the base of the sorogen in the direction of the stipe outlines the boundary of the slime deposited in the process of laying

down the sorogen. The position of this line with relation to the sorogen in the succeeding figures is a good index of the movement of the latter.

Figure 47 is from a photograph taken fifteen minutes later; the apical region of the sorogen has already begun to curve upward without any noticeable antecedent rounding up or change of outlines. The mass has, however, pushed forward and added to the length of the stipe, as is shown by the position of its base in relation to the end of the dark line of amoebae lying along the earlier formed part of the stipe and the relative position of the slime line referred to above.

That the sorogen is curving upward is shown by the dark anterior zone, due to stoppage of the light, the high light on the apex, and the fact that the sorogen as seen from above appears shorter by the amount that it has curved upward. The relations of the parts and the nature of the process would be better shown in a photograph taken from the side but I have not been able, without disturbing it too much, to get a sorogen in position for such a picture.

Figure 48 shows what occurred in the next fifteen minute interval. The upturn of the apex has proceeded still further so that the length of the horizontal part is only about one-half what it was when the experiment began. The further forward movement of the base is shown in relation to the reference points noted above. In this figure the nature of the sorogen as a mass of free amoebae is indicated by the fact that certain of the amoebae have become separated from the mass and are left behind along the stipe. Other amoebae are seen bulging from its sides.

Fifteen minutes later, as shown in figure 49, the sorogen has come to stand almost vertically on end and the basal portion appears much more tapering. The outline of the stipe can be traced, forming the axis of the mass, and the high light spot marks its vertex. In another fifteen minutes (fig. 50) the sorogen has practically regained its position vertical to the substratum. For this figure the negative was exposed at a higher focus and the free amoebae in the culture medium appear as high light spots, etc., due to their being out of focus. In figure 51 the sorogen appears in end view merely as a rounded black mass.

The process by which the pseudoplasmodial mass erects itself

in this case simulates that by which a root or shoot regains its normal geotropic relations when laid in a horizontal position. This latter process has long been known to be a growth curvature. In the case of the young sorocarp there is no growth either in mass or number of cells. As noted, some cells may drop behind in the process, and there is doubtless loss of weight, due in part to destructive metabolism involved in the work done. The stimuli which initiate and direct the reaction are doubtless hygro- and geotropic, and the process is one of specifically oriented motion, the anallactic creeping of the mass of myxamoebae. The sorogen bends upward like a shoot, but the bending is due to the specifically oriented direction of creeping of the myxamoebae. The facts are unmistakable. If, as in the ordinary class experiment to show the growth curvature of a root, you were to lay off on the sorogen of *Polysphondylium* a series of lines at equal distances apart, these distances would not be changed while the curvature was taking place, barring possible slight differences between the convex and concave flanks due to shifting of their position by the individual amoebae.

The recovery of the erect position by the sorogen of *Polysphondylium* is not a growth curvature, and in the light of the facts here we may well question whether specifically oriented tropistic movements involving mass growth and cell multiplication in the root and shoot should not be regarded as determined by intercellular relations analogous to those existing between the free amoebae in the sorogen, rather than by some organismal principle of root or shoot behavior. In both cases the external stimuli of gravity, relative moisture, etc., are the same.

In *Polysphondylium* mass growth is completed in the free swarming stage and is unoriented. The myxamoeba enlarges in three dimensions. Whether division is oriented in the sense that the planes of successive bipartitions would intersect at right angles as in *Pediastrum* is not determined. In any case a specific orientation of the division planes would mean nothing for the organization of the future sorocarp, unless some sort of pattern orientation is assumed to be maintained by the amoebae in all their wanderings and then to further determine their arrangement in the process of stipe and sorus formation, which is scarcely conceivable.

Discussion. When in *Polysphondylium* unoriented mass growth and unoriented census growth have been completed and the myxamoebae have reached what we call the maturity of the fruiting stage, specifically oriented movements begin. Differentiations based in each case on specific positions successively achieved by the cells emerge and lead to the formation of the sorocarp with its definitely oriented position with relation to the substratum, the more or less fixed size relations between its parts, its radial and metameric symmetry, and differentiation into soma and germ plasm. For *Polysphondylium* it is obvious that growth and differentiation, instead of being expressions of an organismal protoplasmic mass, are respectively the processes of cell growth and cell multiplication followed by cell aggregation and cell differentiation in a colony whose unity and organization are matters of specialization in position and function, worked out by the interactions of its component cells.

In the case of the Myxomycetes we have in the true plasmodium an organized mass of protoplasm which, by specifically regulated movements as a mass, may produce stalked fruit bodies quite similar to those of the Acrasieae. However, differentiation never proceeds as far in the Myxomycetes as in the sorocarp of *Polysphondylium* with its whorls of branches and its sharp differentiation of soma and germ plasm. A comparison of the organization of *Stemonitis* with that of *Polysphondylium* shows at once the greater possibilities which go with the colony of free individual cells, as contrasted with the multinucleated protoplasmic mass of *Stemonitis*. The latter is, as I have elsewhere pointed out, functionally, in its reactions and capacity for differentiation, a single cell. Its stipe and capillitial system are secretions. It shows no metamerism nor differentiation of soma and germ plasm. To be sure such coenocytic algae as *Bryopsis* and *Caulerpa* show more complexity of form than does *Polysphondylium*, but that they are at a disadvantage in their capacity to achieve complexity and specialization in organization, as compared with true multicellular plants such as the red algae, will hardly be denied. To claim that, after all, the plant is only a mass of protoplasm, whether cut up into cells or not, is to overlook the obvious facts of organization in the Myxomycetes and Siphoneae as compared with the red or

brown algae and the higher plants, in which the unit of organization and differentiation is in general the uninucleated cell.

Morphogenesis and differentiation in *Polysphondylium* involve cellular phenomena of at least three types: (1) Translocatory, in turn synallactic, anallactic, and diallactic amoeboid creeping movements, by which the pseudoplasmodial mass is formed from the free creeping amoebae and further transforms itself into the mature plant, the sorocarp, with its polar differentiation, its metameric and radial symmetry, and its apical and lateral sori. (2) Specific morphallactic cellular form adjustments at the ends of the elongating stipe and branches, by which the myxamoebae fit themselves together so as to achieve the tapering columnar form of the stipe and branches with their curves and angles adapted to support and maintain the equilibrium of the load of sori. (3) Intracellular histogenetic metamorphoses of the cells *in situ*, in the stipe and in the sori respectively, by which they become vacuolar, expand and become closely pressed together into a parenchyma-like tissue in the stipe and take on the oblong form with dense contents of the spores in the sori.

The third of these phases is the same in principle in these semi-coenobes as in the metaphytes, though, in the latter of course a vastly longer list of tissues is produced. The first generally recognized change in the cells, as you proceed backward from the apical region of a root tip, is vacuolization of the cytoplasm as a simple method of cell enlargement, and Olive has emphasized and made very clear the part which vacuolization plays in the differentiation and enlargement of the stipe cells in these Acrasieae. He has also given in detail the evidence for the development of specialization of the wall in the cells of the stipe, which is also a main factor in the differentiation of the vascular and strengthening tissues in the metaphytes.

The second type of cell changes in these semi-coenobes—the morphallactic form adjustments at the tips of the stipe and branches by which the tapering form of the stipe is achieved and the direction of elongation is so controlled as to maintain the equilibrium of the top-heavy mass and develop the smooth curves and balanced form which is so characteristic—is apparently the most specific for this type of plant. The general adaptive signi-

ficance of the erect and branching habit of *Polysphondylium* is plainly that of securing better distribution of the spores. The Sorophoreae, as both Olive's work and that of earlier students of the group has shown, present a well defined evolutionary series of types in which elevation of the sori above the substratum is obviously a factor of high selective value. The reversal of the hygrotopic relations of the species as they pass from the vegetative myxamoeboid stage to that of maturity and spore dissemination is a long known fact for the group.

Parr (1926) has attempted to bring greater clarity into the discussion of adaptations by pointing out that adaptation is a relation between an organism and its environment, rather than a character of either the organism or its environment. However this question of verbal usage may be, the adaptive relation for spore dissemination is plainly an achievement, both in the phylogeny of the group and in the species, worked out by the specific reactions of the myxamoebae to their environment. The development of the series is highly adaptiogenetic rather than simply orthogenetic, and the interrelations of form and function are well illustrated. Of more theoretic interest perhaps is the fact that in this process of aggregation and differentiation we have in very simple form an example of the nature of integration and organization by which out of a manifold of unit individuals an individual of another order arises.

To many it would appear that we have no adequate working hypothesis as to the nature of somatic segregation and differentiation. Granting the genic transmission of the *Anlage* for the characters of adult plants and animals we are still wholly at a loss to account for the working out and expression of these characters in ontogeny (Lillie, 1927.)

Heidenhain (1923) feels that the development of the cell theory has resulted only in an analysis of the biological problem, and that further progress must involve attempts at least at synthesis. From this standpoint he has developed his conception of the biosystems, briefly: (1) centrioles, chromioles, etc.; (2) chromosomes, etc.; (3) nuclei; (4) cells; (5) muscles, nerves, etc.; (6) units of symmetry, metameres, antimeres, etc. The development of *Polysphondylium* may be well expressed in terms of such a series, and it further shows that the successive transitions in such

an ascending scale are achieved in each instance by the integrating activity of the cells themselves.

Whether Bertalanffy (1928), with his postulated immanent biologic factors for form, has escaped the vicious circle of neovitalism may be a matter of dispute. The obvious fact as to *Polysphondylium* is that we have in its development a case of integration, in which the manifold (the swarm of amoebae) emerges into the unity of a higher order as an expression of the interrelated and coördinated activities of the cell units. The form determining moments or organizing principles, if such there be, reside obviously in the myxamoebae rather than in the erect, axially elongated, metameric and radially differentiated and symmetrical sorocarp.

It is to be hoped that Bertalanffy will soon give us the further part of his analysis which he suggests (p. 213) and which is to deal with the morphogenetic significance of the hormones and other agencies of chemical interrelations between cells, tissues, and organs, as well as the effects of nerve stimuli, functional activity, etc. Bertalanffy excuses this omission partly on the ground that he is first concerned with the ultimate and 'primary form building processes' and that these chemical and other interrelations in the organism are essentially matters of functional coördination which, as it were, presuppose organization. In the last analysis morphogenesis, aside from differentiation, in the metaphytes is a matter of specifically oriented cell enlargement and specifically oriented cell divisions, however they may be determined. That hormones do determine such processes in many cases is becoming more and more clear, as well as the fact that growth stuffs may determine tropistic curvatures. One can hardly question that the problems of form development in these semi-coenobes appear in relatively simple form and that the organization achieved in the sorocarp is in its structural constitution simple and primary for plants. The sorocarp of *Polysphondylium*, with its erect tapering stem, branches, and fruits, is as it were a diagram of the cormophyte as seen in ferns and seed plants. That, however, chemical interrelations between the cells are basic for the synallactic aggregation stages in *Polysphondylium* seems to be a natural assumption. Chemical stimuli may be also involved as well as contact, pressure, and weight rela-

tions in the morphallactic cell adjustments by which the stipe and branches are built and the general equilibrium of the sorocarp is maintained.

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Explanation of plates 5-9

All the figures are of *Polysphondylium violaceum* Bref., and the photographs were made with the Zeiss apochromatic objectives and compensating oculars and the Zeiss microplanars.

PLATE 5

Figures to show general habit and variation in size and proportions. Magnification about 50 diameters except as noted.

Figs. 1, 2. Unbranched sorocarps like those of *Dictyostelium*.

Fig. 3. Sorocarp with a single branch.

Fig. 4. Sorocarp with single lateral sorus with no stipe or a very short stipe.

Fig. 5. Sorocarp with one whorl of three branches.

Fig. 6. Two sorocarps very close together at base. The one to the right unbranched, the other with a single whorl of three branches placed unusually close to the terminal sorus. The figure also shows at the lower right hand corner a single sorus and part of the stipe of another plant.

Fig. 7. Sorocarp with whorl of three branches and at the node above a single branch.

Fig. 8. Sorocarp with whorl of three, and one with whorl of two branches. Internode unusually short.

Fig. 9. Sorocarp with two whorls of four branches each.

Fig. 10. Rather normally proportioned sorocarp with two whorls, one with four and one with three branches.

Fig. 11. Sorocarp with five whorls of branches.

Fig. 12. Sorocarp with eight whorls of branches. Number of branches per whorl varies from one to six.

Fig. 13. Sorocarp with eight whorls of branches. \times about 60.

Figs. 14, 15. Two sorocarps each with seven whorls of branches. \times about 20.

Fig. 16. Sorocarp with eleven whorls of branches, with from two to four branches per whorl. \times about 20.

* PLATE 6

Myxamoebae and stages of aggregation to form the pseudoplasmodium. Figs. 17 and 18 with apochromatic objective 8 mm., compensating ocular 12. Figs. 19-22 microplanar 3.5 cm.

Fig. 17. Myxamoebae in free swarming stage, movement rather sluggish. Exposure 5 sec. \times about 400.

Fig. 18. Myxamoebae more active, tending to elongate. Exposure 5 sec. \times about 375.

Fig. 19. Central region of a pseudoplasmodium showing synallactic flowage to a center at which a sorocarp is to be formed. \times about 40.

Figs. 20, 21. A later stage of development of the same pseudoplasmodium, in which the young sorocarp shows in the photograph as a blunt projection from the central mass. Figure 21 is more highly magnified and was taken only a few minutes later.

Fig. 22. Young sorocarp arising from a rather one-sided pseudoplasmodium. The dark line extending diagonally across the figure is the basal portion of the stipe of another sorocarp.

PLATE 7

Young sorocarps showing anallactic upward movement and diallactic plagiotropic branch formation. Photographed with microplanar 3.5 cm.

Fig. 23. Young sorocarp. Stipe about twice the length of the sorogen.

Figs. 24, 25, 26. Three stages in development of same sorocarp, showing successive abstriction of segmental masses from the apical sorogen.

Figs. 27-31. Four stages in branch formation of the same sorocarp. Photographs taken at intervals of ten to twenty minutes. At the same time the apical sorogen has bent over until it touched the substratum, and then changed its direction of motion and begun to regain its position vertical to the substratum.

Figs. 32, 33, and 34 show various stages in the development of the segmental masses into whorls of branches.

PLATE 8

The formation of the stipe and branches. All figures taken with the Zeiss 8 mm. objective and compensating ocular 12.

Fig. 35. Base of stipe irregular in outline and turned to one side.

Fig. 36. Segment of same stipe in median region; tapering slight.

Fig. 37. Apical segment of a stipe showing slight thickening where enclosed in the terminal sorus.

Fig. 38. Lateral stipe with strongly bulbous base.

Fig. 39, 40, 41, 43. Lateral stipes with less bulbous swelling at base.

Fig. 42. Shows one complete lateral stipe and the bases of two others in the same whorl.

Fig. 44. Shows a lateral stipe consisting of a single row of cells. The tapering is determined entirely by the form of the cells.

Fig. 45. Shows the bases of three branches in a whorl with different degrees of bulbous enlargement.

PLATE 9

Illustrations of organic regulations in *Polysphondylium*. Figures 52 to 60 were made with Zeiss microplanar 3.5 cm.

Figs. 46-51 show stages by which the sorogen of a young sorocarp when laid horizontal on the substratum turns up by anallaxis until it has regained the vertical position. The pictures were taken with Zeiss apochromatic objective 16 mm. compensating ocular 8, at intervals of about fifteen minutes.

Fig. 52. Fragment of stipe with amoebae adhering to it from young sorocarp teased up and mounted in hanging drop.

Fig. 53. The same preparation after about seventy-five minutes.

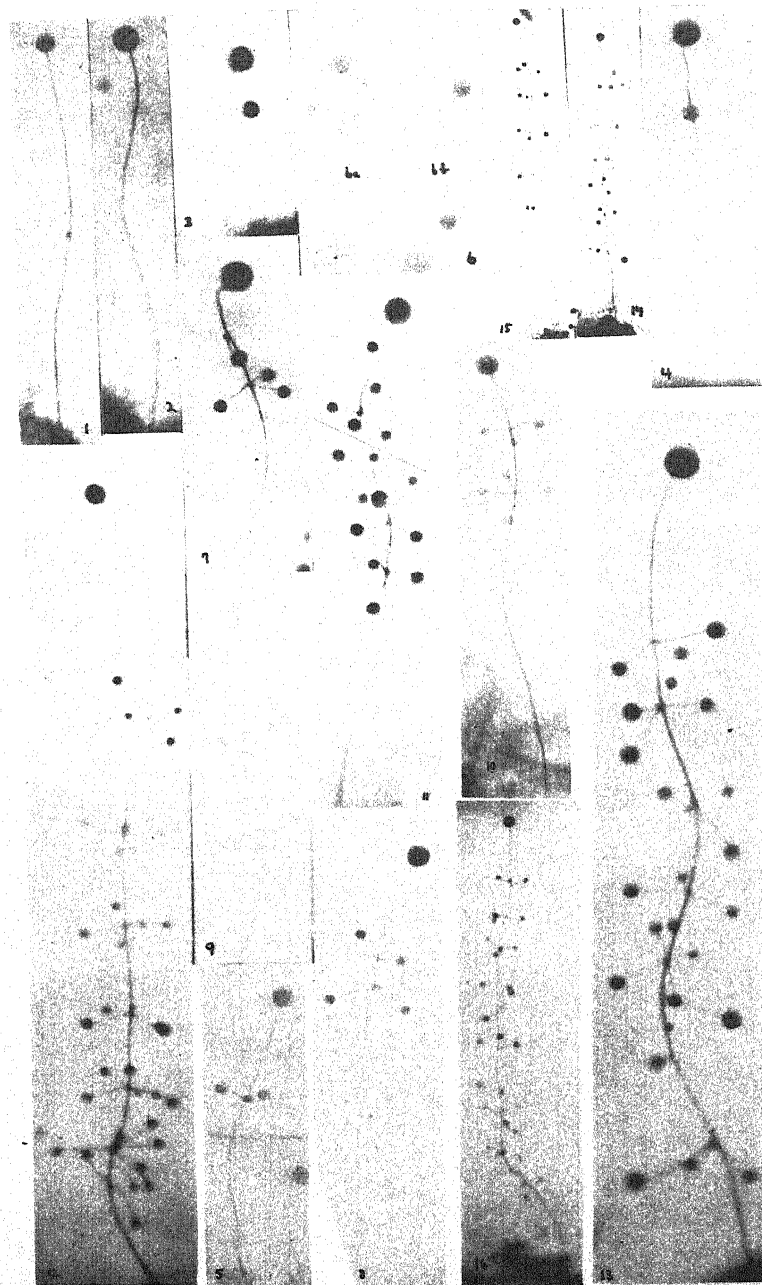
Fig. 54. The same preparation after about fourteen hours.

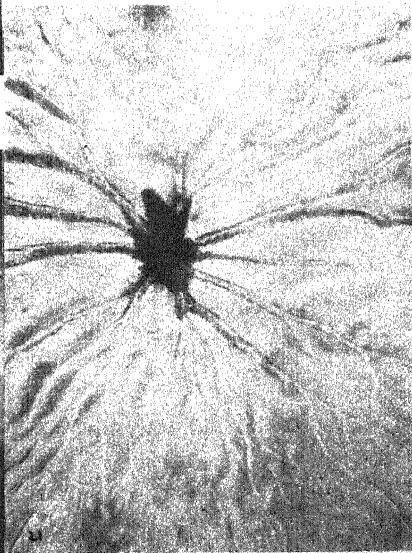
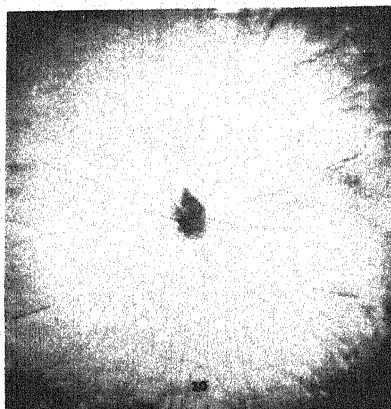
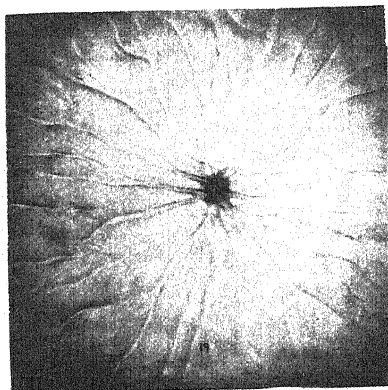
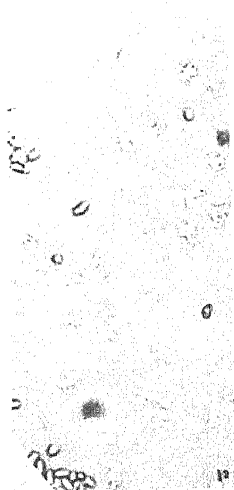
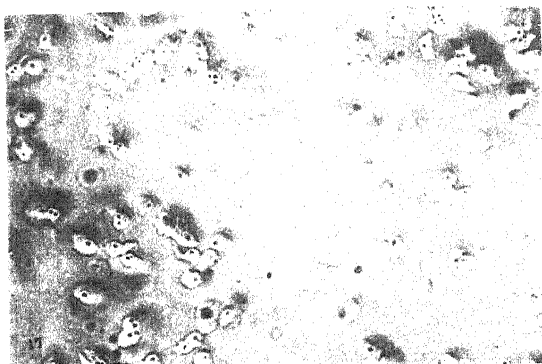
Fig. 55. Two masses of amoebae teased off from a young sorocarp.

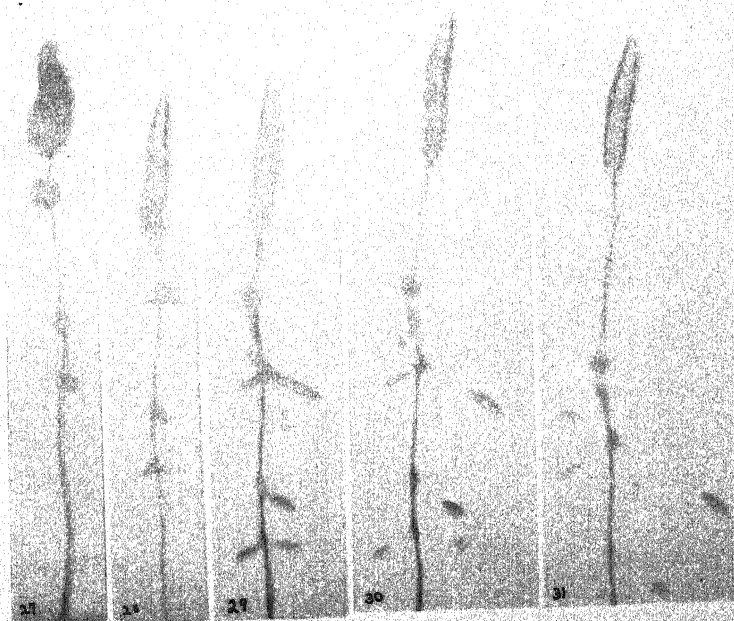
Fig. 56. The same one hour later.

Fig. 57. One of two sorocarps formed during the next twelve hours from the upper one of the masses of amoebae shown in the two previous figures.

Figs. 58-61. A similar series to that shown in figures 52-54.







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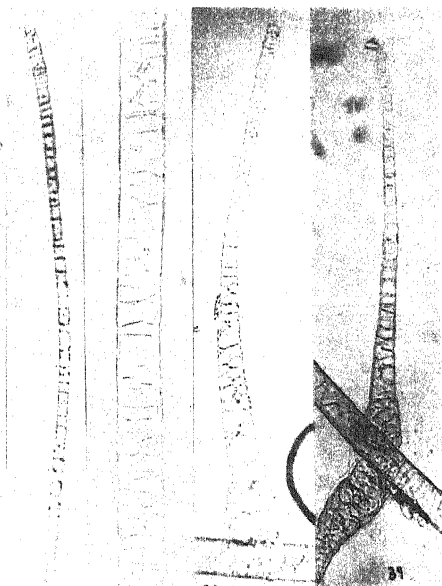


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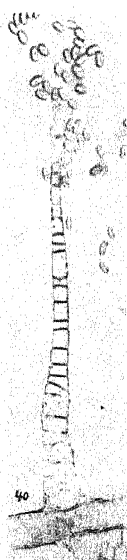
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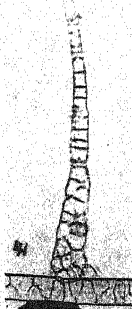
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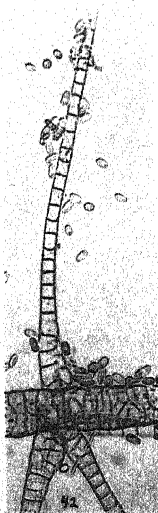
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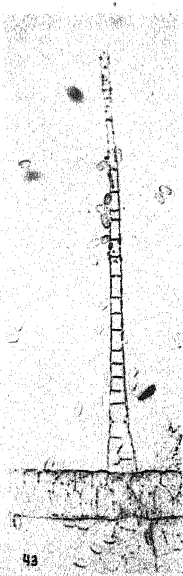
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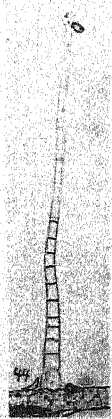
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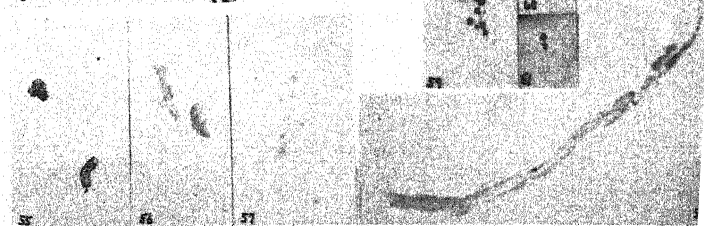
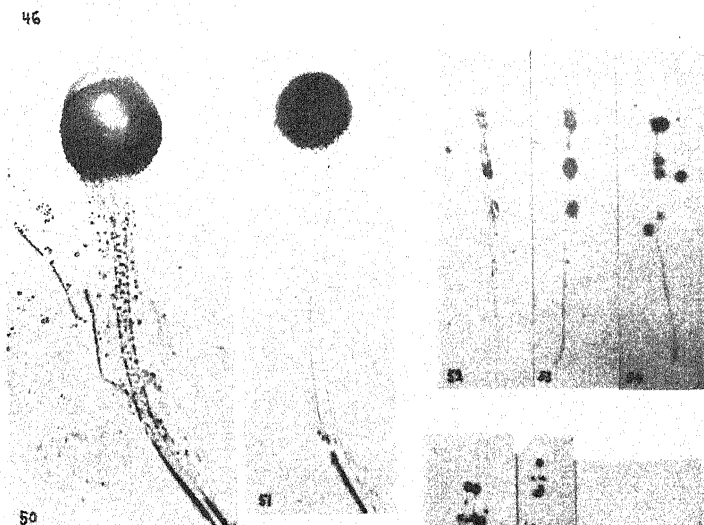
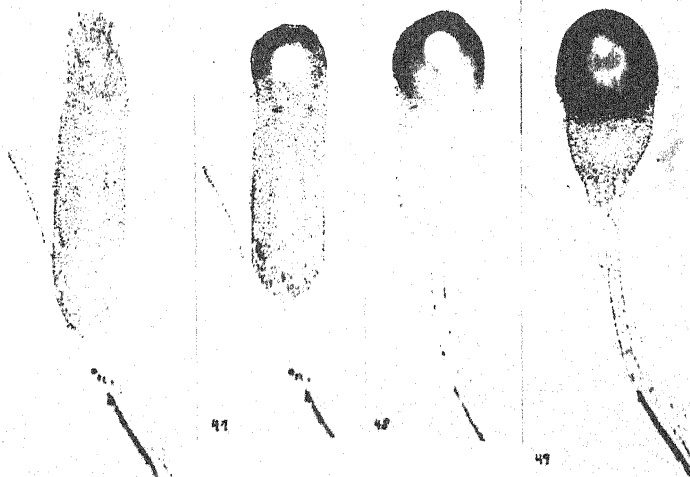


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Histology of the wood of angiosperms

I. The nature of the pitting between tracheary and parenchymatous elements

FREDERICK H. FROST¹

(WITH PLATE 10)

During the course of an investigation of the structure of the wood of our native arborescent angiosperms the writer has observed several features which warrant separate treatment. The type of pitting found when a vessel segment, tracheid, or fiber lies adjacent to a xylem parenchyma or ray parenchyma cell will be discussed in this instance.

The following quotation from Solereder (6) summarizes the present status of opinion in respect to this point.

These walls (walls of contact between a vessel segment and a parenchymatous cell) are occupied (a) either by one-sided bordered pits (half-bordered in the common terminology) one or more² of which corresponds to large one-sided simple pits on the adjoining parenchyma-wall, or (b) by one-sided simple pits of varying size which correspond to pits of equal dimensions on the wall of the adjoining parenchyma cell.

In other words, the wall of a parenchymatous cell in this situation possesses simple pits, while the vessel wall may have either bordered or simple pits. Similar statements may be found in the classical texts of Strasburger (7), De Bary (1), or Haberlandt (3), in the more recent texts such as Eames and MacDaniels (2), or Jeffrey (4), and in works dealing with the detailed structure of wood, such as Record (5).

It is undoubtedly due to the very concise statements of the above investigators that a thorough study of these pits has not been made and their true nature described in detail.

MATERIALS AND METHODS

The sections used in this investigation average about five microns in thickness and were stained *lightly* in Haidenhain's iron-alum haematoxylin and safranin. It is essential, if the de-

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² See figures 1, 2. This condition is due to the breaking up of scalariform pitting into opposite pitting and is common in species with scalariform perforations.

tails of the pitting are to be clear, that the staining is light and that both the haematoxylin and safranin are destained. The wood was softened with hydrofluoric acid but was not embedded. Properly softened wood will nearly always cut as thin as five microns if the microtome knife is in excellent condition. The nature of the pitting was, of course, determined in section, as it is impossible, in most cases, to distinguish between a half-bordered pit and a fully bordered pit in face view.

OBSERVATIONS AND DISCUSSION

It is an almost universal rule that the same type of pitting exists, in a given species, between the ray parenchyma and tracheary elements and xylem parenchyma and tracheary elements. For this reason the discussion which follows applies to both ray and xylem parenchyma.

The pitting of vascular parenchyma³ cells, when adjacent to vessel segments, falls into four main groups as regards the outline of the pits in face view. These pits may be scalariform, as in *Gordonia lasianthus* Ellis (fig. 1) and many other primitive woods; reticulate, which is transitional between the scalariform and opposite types, as is found occasionally in *Sambucus Simpsonii* Rehder (fig. 2); opposite, as is frequently the case in *Carpinus caroliniana* Walter (fig. 3); or alternate, as is well illustrated in *Acer floridanum* (Chapman) Pax (fig. 4).

In section the vessel-vascular parenchyma pits, when scalariform in face view, are very often fully bordered. This condition is typical of *Gordonia lasianthus* Ellis (figs. 5, 6) and *Liquidambar styraciflua* Linnaeus (fig. 13). The scalariform-half-bordered condition is shown very clearly in *Symplocos chiriquensis* Brand (fig. 7). Scalariform simple pits are, as one would expect, quite rare, and if found are usually associated with half-bordered pits or fully bordered pits. Figure 8 illustrates these pits from *Anacardium excelsum* Skeels.

The reticulate or intermediate type of pitting may be fully bordered, half-bordered, or simple. Illustrations of these types may be found, in the same order as above, in the following species: *Magnolia acuminata* Linnaeus in part, *Dalea spinosa* Gray,

³ The term 'vascular parenchyma' is here used to denote both ray and xylem parenchyma.

and the reticulate simple pits occasionally occur in *Trema mollis* Loureiro. In the latter species the pits are usually one-half bordered.

Likewise the opposite or alternate type of pitting may be fully bordered, half-bordered, or simple. Excellent bordered pits of these two types may be found in *Ostrya Knowltonii* Coville (fig. 9, a, b). Very distinct half-bordered pits occur in *Hicoria pecan* Britton (fig. 10), and simple pits are quite common in *Sambucus coerulea* Rafinesque (fig. 11).

The writer has observed bordered pits in parenchymatous cells in a number of other genera, both tropical and temperate, and it is certain that the occurrence of these types are not abnormalities,⁴ but are consistent features of the structural elements of wood. The sequence of changes which these pits undergo during the course of evolutionary specialization will be treated in detail in a later paper.

The pitting between parenchymatous elements and fibers is not abundant and the pits are generally small. Pits between libriform fibers (libriform fibers have simple inter-fiber pits) and parenchyma cells are always simple (fig. 16, *Sambucus callicarpa* Greene). Pits between tracheids or fiber tracheids and parenchyma cells, on the other hand, may be bordered, half-bordered, or simple, since the inter-fiber pits are always bordered.

Bordered pits in this situation are found quite frequently and are very clear in thin and properly stained preparations of *Gordonia lasianthus* Ellis (fig. 12), *Platanus Wrightii* S. Watson, and *Liquidamber styraciflua* Linnaeus (fig. 13). The half-bordered pit is quite common and is illustrated by *Malus coronaria* Miller (fig. 14). The simple type is found in *Betula lenta* Linnaeus (fig. 15) with the half-bordered type. The writer has not observed simple pits in this situation in woods which possess fibers with well developed bordered inter-fiber pits.

From the foregoing notes and the writer's observations it is clear that the type of pitting between a tracheary element and parenchymatous element is determined to a large extent by the degree of specialization of the tracheary element rather than the

⁴ Thompson, W. P., Bot. Gaz. 53: 331-358, describes and figures a ray parenchyma cell from *Abies* with bordered and simple pits. Cells of this type have also been described from *Sequoia*.

parenchymatous element. Exceptions to this rule occur in groups which possess the heterogeneous type of ray, in which cases the upright ray parenchyma cells often show a different type of pitting than the radially elongate ray parenchyma elements.

The details of pitting, of the types above described, are useful in wood identification studies, since they increase the number of possible characteristics a plant may possess. In transitional genera, such as *Sambucus*, it is possible to differentiate easily between certain species by the occurrence of bordered or simple vessel-ray pits.

It is likewise possible to distinguish between the North American species of *Ostrya* and *Betula* on the basis of the pitting between fibers and xylem parenchyma, but in closely related genera like *Liriodendron* and *Magnolia* or *Salix* and *Populus* the details of the pittings are usually identical. The type of vessel-ray or fiber-parenchyma pitting as a rule is more apt to be characteristic of a subfamily or family than of the individual species of a genus in our native arborescent angiosperms.

SUMMARY

1. The prevalent conception of the type of pitting which occurs between tracheary and parenchymatous elements in the secondary xylem of angiosperms is incorrect.

2. Fully bordered, half-bordered, and simple pits are characteristic features between tracheary cells and vascular parenchyma.

3. The type of pitting on the wall of the parenchyma cell is controlled largely by the degree of specialization of the vessel or fiber which lies next to it.

4. The detailed structure of pits of this nature is useful in wood identification.

In conclusion the writer wishes to express his appreciation to Professor I. W. Bailey for many kindnesses.

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Explanation of plate 10

(*v.s.* refers to vessel segment; *x.p.* to xylem parenchyma; *r.p.* to ray parenchyma; and *t.* to tracheids or to fibers.)

Fig. 1. *Gordonia lasianthus*. Scalariform vessel-ray pits. Radial Section.

Fig. 2. *Sambucus Simpsonii*. Reticulate vessel-ray pits. Radial section.

Fig. 3. *Carpinus caroliniana*. Opposite vessel-ray pits. Radial section.

Fig. 4. *Acer floridanum*. Alternate vessel-ray pits. Radial section.

Fig. 5. *Gordonia lasianthus*. Bordered fiber-ray and fiber-parenchyma pits. Scalariform bordered vessel-parenchyma pits. Transverse section.

Fig. 6. *Gordonia lasianthus*. Scalariform bordered vessel-ray pits. Tangential section.

Fig. 7. *Symplocos chiriquensis*. Scalariform half-bordered vessel-ray pits. Tangential section.

Fig. 8. *Anacardium excelsum*. Scalariform simple vessel-ray pits. Tangential section.

Fig. 9. *Ostrya Knorzeltonii*. (a) Opposite bordered vessel-parenchyma pits. (b) Opposite bordered vessel-ray pits. Radial and tangential section.

Fig. 10. *Hicoria pecan*. Opposite half-bordered vessel-ray pits. Tangential section.

Fig. 11. *Sambucus coerulea*. Alternate simple vessel-ray pits. Tangential section.

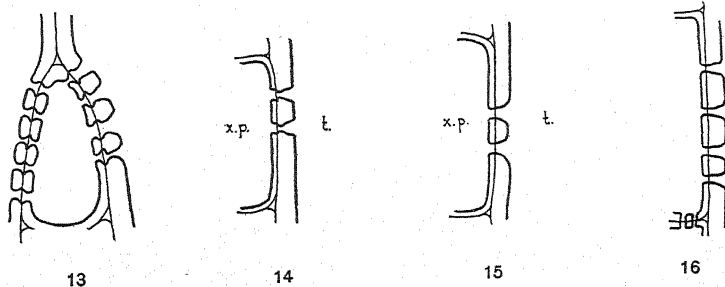
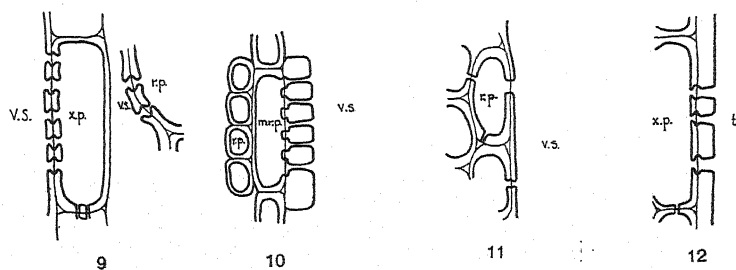
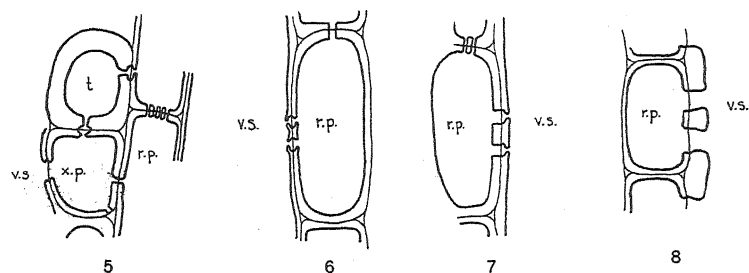
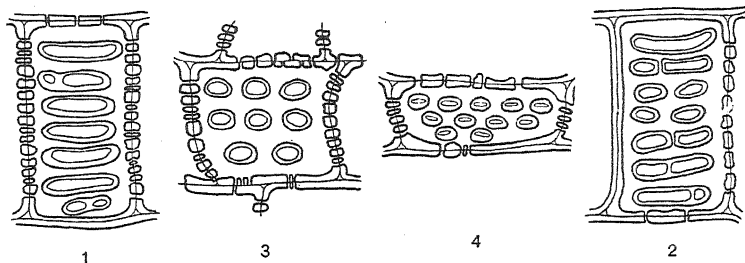
Fig. 12. *Gordonia lasianthus*. Bordered fiber-parenchyma pits. Radial section.

Fig. 13. *Liquidamber styraciflua*. Bordered fiber-ray pits and scalariform bordered vessel-ray pits in the same cell. Tangential section.

Fig. 14. *Malus coronaria*. Half-bordered fiber-parenchyma pits. Radial section.

Fig. 15. *Betula lenta*. Simple fiber-parenchyma pits. Radial section.

Fig. 16. *Sambucus callicarpa*. Simple pits between libriform fiber and xylem parenchyma. Radial section.



The genus *Viburnum* in northwestern South America

E. P. KILLIP AND A. C. SMITH

In attempting to identify a large series of specimens of *Viburnum* which we collected in eastern Colombia, we found that nearly all the Andean material of this genus in American herbaria had been referred to *V. glabratum* H.B.K., though quite obviously several species were represented. Monographers apparently have paid little attention to the South American representatives of the genus, confining themselves almost wholly to the species occurring in the North Temperate regions. Several Peruvian species were recently described by Graebner, but these appear to be local species which do not range into the northern part of the Andes.

As in the case of the species from North America and the Old World, the principal diagnostic characters lie in leaf-shape, indument, and size and branching of the corymbs, the flowers and fruits showing little variation.

The herbaria in which specimens we have examined are deposited are indicated thus: Arnold Arboretum (A); Field Museum of Natural History (F); Gray Herbarium of Harvard University (G); Royal Botanic Gardens, Kew (K); U. S. National Herbarium (N); New York Botanical Garden (Y).

KEY TO SPECIES

Lower surface of leaves uniformly pubescent with stellate hairs, usually at least 5 per sq. mm. of surface on mature leaves.

Leaf hairs straight (.3-6 mm. long); corymbs wide-spreading, more than 8 cm. wide, often 13 cm.....1. *V. lasiophyllum*.

Leaf hairs crispate (.15-3 mm. long); corymbs smaller, rarely more than 10 cm. wide, usually less than 8 cm.

Plants of lax habit, with elongate branches; inflorescence 3- or 4-times branched; leaves rarely in threes.....2. *V. pichinchense*.

Plants compact, the branches short; inflorescence twice-branched; leaves often in threes.....2a. *V. pichinchense toledense*.

Lower surface of leaves essentially glabrous, sometimes pilosulous in axils of nerves.

Branchlets and rays of inflorescence densely canescent-pulverulent.

3. *V. glabratum*.

Branchlets and rays of inflorescence glabrous or with various indument, not pulverulent.

Leaves thick coriaceous, often in threes.....4. *V. triphyllum*.

Leaves herbaceous, never in threes.

Leaves broadest above the middle.

Branchlets essentially glabrous; petioles about 15 mm. long; bractlets persistent, up to 7 mm long; calyx tube densely glandular-punctate.5. *V. apiculatum*.

Branchlets rufo-tomentose; petioles less than 10 mm. long; bractlets deciduous, about 2 mm. long; calyx tube sparingly glandular-punctate.6. *V. suratense*.

Leaves broadest below or near the middle.

Leaf margins slightly revolute and appearing to be regularly ciliate.7. *V. fragile*.

Leaf margins flat and obviously not ciliate.

Apex of leaves obtuse (rarely obtusely acuminate).

Branchlets and rays of inflorescence glabrous or sparingly appressed-hirtellous, bractlets about 3 mm. long.

Leaves more than 7 cm. long; texture herbaceous....

8. *V. leptophyllum*.

Leaves less than 7 cm. long; texture thin herbaceous.

8a. *V. leptophyllum venezuelense*.

Branchlets and rays of inflorescence densely rufo-tomentose with matted hairs; bractlets about 1.5 mm. long.

Corymbs less than 10 cm. wide, the rays straight, stout, ascending; branchlets stout.9. *V. floccosum*.

Corymbs more than 10 cm. wide, the rays flexuose, slender, divaricate; branchlets slender....10. *V. divaricatum*.

Apex of leaves sharp-acuminate or long-acuminate.

Leaves twice as long as broad.

Corymbs ebracteate and ebracteolate; calyx lobes semi-circular, finely and regularly ciliate....11. *V. cornifolium*.

Corymbs deciduously bracteate and bracteolate; calyx lobes ovate, smooth at the margins or slightly ciliate.

12. *V. Lehmannii*.

Leaves three times as long as broad13. *V. Toronis*.

DESCRIPTIONS OF SPECIES

1. *VIBURNUM LASIOPHYLLUM* Benth. Pl. Hartw. 189. 1845. Shrub 3-4-m. high; branchlets subterete, densely and softly stellate-ferruginous-tomentose, the internodes 4-7 cm. long; petioles 8-13 mm. long; leaves broadly ovate or oblong-ovate, 4-7 cm. long, 3-6 cm. wide, acute or abruptly acuminate at apex, subcordate at base, obscurely sinuate-dentate or subentire in upper half, entire in lower half, stellate-pubescent with straight hairs (.3-.5 mm. long), the pubescence much denser and softer beneath, the nerves scarcely impressed above; corymbs sessile or pedunculate, 8-12 cm. wide, pubescent as the branchlets, bracteate with soon deciduous linear

bracts (about 5 mm. long), 5-8-rayed (primary branches 2-4 cm. long), 3- or 4-times branched, bracteolate, the bractlets linear-oblong, 3-4 mm. long, persistent; calyx tube about 1.5 mm. long, sparingly glandular-punctate and pubescent with scattered short stiff hairs, the lobes triangular, about 1 mm. long, subacute, strongly ciliate; corolla about 2 mm. in diameter at the base, 3-4 mm. long, the lobes oblong-ovate, 2 mm. wide; ovary furrowed.

COLOMBIA: Cundinamarca: Pacho, *Hartweg 1041* (type; N, fragment and photo; Y, photo). Other specimens are: *Pennell 2474* (Y), from Sibaté, and *Appollinaire & Arthur 76* (N), from Gaudalupe, both in the same general locality as the type, which differ in having proportionately narrower leaf blades with petioles less than 5 mm. long.

2. *V. PICHINCHENSE* Benth. Pl. Hartw. 188. 1845. *V. Urbani* Graebn. Bot. Jahrb. 37: 435. 1906. Shrub 2.5 to 4 m. high, much branched, the branches elongate, up to 8 meters long; branchlets and rays of inflorescence ferruginous-stellate-tomentose with crispate tangled or matted hairs .15-.3 mm. long; petioles .5-1.5 cm. long; leaves ovate, oblong, or slightly obovate, 8-12 cm. long, 4-6 cm. wide, acute or abruptly acuminate at apex, rounded at base, entire or subentire, impressed-nerved and sparingly stellate-pubescent above, rufo-stellate-tomentose beneath, the hairs like those of the branchlets; corymbs pedunculate, 4-7 cm. wide (occasionally up to 9 cm.), ebracteate (or sometimes with large ovate-lanceolate bracts), 5-7-rayed (primary rays .5-2.5 cm. long), 3- or 4-times branched, bracteolate (the bractlets linear, up to 3.5 mm. long, deciduous) calyx tube about 1.2 mm. long, sparingly glandular-punctate or nearly glandless, the lobes triangular, .5-.7 mm. long, acute, strongly ciliate; corolla about 1.3 mm. in diameter at base, 2.8-3 mm. long, the lobes rounded, about 1.7 mm. wide; ovary terete; fruit broadly ovoid, 6-8 mm. long, 5-6 mm. in diameter, black.

COLOMBIA: El Cauca: Near La Topa and El Pedegral, Central Andes, east of Popayán, 1300-1600 m., *Lehmann 5161* (N, photo of type of *V. Urbani*; K). San José, west of Popayán, 2600 m., *Pennell & Killip 7383* (N,Y). Escaleretas, Río Paez basin, 2500-3000 m., *Pittier 1356* (N). Near Popayán, 1800 m., *Lehmann 831* (N), 3548 (N), 7941 (F).—ECUADOR: Mt. Pichincha, *Hartweg* (N, photo and fragment of type; Y, photo). Cuenca: Chagal, 2000-2500 m., *Lehmann 7940* (N, photo; K. Cited as *V. anabaptista* Graebn. in Bot. Jahrb. 37: 435).

Perhaps more than a single species is represented by the material here cited, but we have not been able to find reliable characters upon which separate species can be based. Apparently the habit of the plants is quite variable. Lehmann's 5161, the type of *V. Urbani*, is said to be a liana-shrub with elongate branches. *Viburnum pichinchense* is merely described as a shrub, 8 to 12 feet high, but the type specimen suggests a plant of rather lax habit. The plants of Norte de Santander, which we place in the following subspecies, were all compact shrubs with short branches.

The Pennell & Killip specimen from southwestern Colombia closely agrees with the type specimen from Mt. Pichincha. In other material from that region the pubescence is less dense on the under surface of the leaves, which are broader and more noticeably denticulate. Pittier's 1356 has large persistent bracts up to 1.5 cm. long. Graebner referred Lehmann's 7940 to *V. anabaptista*, a Costa Rican species. A specimen of this, courteously lent by the Director of the Royal Botanic Gardens, Kew, agrees closely with other material here placed in *V. pichinchense*.

2a. *Viburnum pichinchense toledense* subsp. nov. Compact shrub or small tree, 3-6 m. high, with short branches; leaves in two's and three's, ovate or oblong-ovate, 4-7 cm. long, 2.5-5 cm. wide, very densely grayish- or rufo-tomentose below, strongly impressed-nerved above; inflorescence twice-branched, few-flowered.

Type, Killip & Smith 20589, collected March 12, 1927, on east-ern slope of Páramo del Hatío en route from Toledo to Pamplona, alt. 2800 m., Dept. Norte de Santander, Colombia, and deposited in the U. S. National Herbarium (no. 1,355,614). Duplicates at A, G, Y. Other specimens are: Norte de Santander: Divide between Río La Teja and Río Mesme, 2800 m., Killip & Smith 19911 (A, G, N, Y). Toledo, 1800 m., Killip & Smith 20107 (A, G, N, Y). Tapatá, 2300 m., Killip & Smith 20184 (A, G, N, Y). Páramo del Hatío, 2900 m., Killip & Smith 20615 (A, G, N, Y).

This may be specifically distinct from *V. pichinchense* on the basis of its compact habit and smaller leaves, which are often in three's.

3. *VIBURNUM GLABRATUM* H. B. K. Nov. Gen. et Sp. 3: 428. 1818. Tree; branchlets, rays of inflorescence, and petioles densely canescent-pulverulent; petioles 5-8 mm. long; leaves ovate-oblong, 8-13 cm. long, 4-5 cm. wide, obtusely acuminate at apex,

rounded at base, entire, glabrous, occasionally canescent-pulverulent on the nerves above; corymbs 5-10 cm. wide, bracteate (bracts ovate-oblong, about 1.5 cm. long, soon deciduous), 6- or 7-rayed, 2- or 3-times branched, bracteolate, the bractlets deciduous; calyx tube about 1 mm. long, essentially glabrous, the lobes .5-.6 mm. long, obtuse or acute, short-ciliate towards apex; corolla about 1 mm. in diameter at base, 1.7-2 mm. long, the lobes ovate, rounded, 2 mm. wide; fruit globose-ovoid, 5-7 mm. in diameter.

COLOMBIA: Cundinamarca: Fusagasugá, *André K444* (Y). Quetamé, 1400 m., *Pennell 1760* (N, Y). Huila: Neiva, 1500 m., *Rusby & Pennell 955* (N, Y). Tolima: Ibagué ?, 1000-1500 m., *André K445* (F, Y). Ibagué, *Hazen 9536* (N, Y).

By far the greater part of the Andean material of *Viburnum* has been referred to this species, apparently with little justification. The description of the indument of the type specimen as 'tenuiter canescenti-pulverulentes' applies only to a small part of the specimens examined in connection with this revision, and in Columbia true *V. glabratum* apparently has only a limited range. The original description states that the plant has two or three bracts, similar to the leaves but smaller. In *Pennell's* no. 1760 and *André's K445* these bracts are present, but in the other material here cited they are wanting, though quite possibly they may have been present at an earlier stage.

4. *VIBURNUM TRIPHYLLUM* Benth. Pl. Hartw. 189. 1845. Shrub or small tree; branchlets terete, hirsute with simple or usually stellate hairs or glabrescent; leaves often in three's (especially the upper ones), ovate or ovate-oblong, 4-8 cm. long, 2-5 cm. wide, rounded or acutish at apex and base, entire, thick-coriaceous, lustrous, glabrous or usually hirsute-tomentose in the axils of the nerves beneath, the nerves usually impressed above; peduncles stout, 3-6 cm. long; corymbs sometimes bracteate, 4-7 (rarely to 9) cm. wide, 6-8-rayed, 2- or 3-times branched, the rays rufo-hirtellous with simple or stellate hairs; calyx tube 1.6-1.8 mm. long, sparingly glandular-punctate, the lobes about 1 mm. long, subacute, ciliate; corolla about 1.5 mm. in diameter at base, 3.7-4 mm. long, the lobes oblong, rounded, about 2.1 mm. wide; fruit ovoid.

COLOMBIA: Cundinamarca: Zipaquirá, *Hartweg 1040* (Y, type collection, N, photo). Bogotá, 2900 m., *Pennell 2006* (Y); *Dawe 156* (N); *Ariste Joseph B105* (N); *Holton 443* (Y). Chiquin-

quirá, *Ariste Joseph* B106 (N). La Calera, *Ariste Joseph* A501 (N). Antioquia: Peñol, 2500 m., *Lehmann* CCXV (N). El Cauca: Paletará to Calaguala, 3100 m., *Pennell* 7102 (N, Y). Coconuco, 2500 m., *Killip* 6804 (N).—ECUADOR: Carchi: Ibarra, 3000 m., *Hitchcock* 20940 (N, Y). Loja: Tablon de Oña, *Rose* 23097 (N, Y). Azuay: Cuenca, *Jameson* (N).

This species is readily recognized by the very thick, coriaceous leaves, which frequently are in three's. The corymbs are more compact than in other close relatives. Much material usually referred to *V. glabratum* belongs to this species.

5. ***Viburnum apiculatum*** sp. nov. Shrub, up to 5 m. high, with large, profusely ramified branches; branchlets terete, essentially glabrous; petioles about 1.5 cm. long; leaves 'sea-green,' obovate, rarely oblanceolate, 5-12 cm. long, 4 to 5.5 cm. wide, cuspidate or apiculate at apex, subacute at base, subentire or sinuate-denticulate, glabrous above, stellate-tomentose on under side along midnerve, the nerves 5 or 6 to a side, parallel, nearly straight, anastomosing close to margin; peduncles stout, 5 to 7 cm. long, minutely stellate-tomentose towards apex; corymbs bracteate (bracts linear, about 1 cm. long), 10 cm. wide, 6-rayed, 2- or 3-times branched (ultimate branchlets very slender), finely stellate-tomentose, bracteolate, the bractlets linear-spatulate, about 7 mm. long, 1.5 mm. wide, acute; calyx tube 1.1-1.3 mm. long, densely glandular-punctate, the lobes ovate, about .9 mm. long, acute, not ciliate; corolla 'white, frequently washed over with pink,' 1.8 mm. in diameter at base, about 4 mm. long, the lobes oblong, rounded, 2.1 mm. wide.

Type, *Lehmann* 5160, collected at Coconuco, east of Popayán, Department El Cauca, Colombia, alt. 2200-2700 m., and deposited in the U. S. National Herbarium (no. 1,420,308). Duplicate F.

6. ***Viburnum suratense*** sp. nov. Tree 3-6 m. high, with a slender trunk, the branchlets terete, sparingly to densely rufo-stellate-tomentose; petioles 5-10 mm. long; leaves obovate or oblanceolate, 5-10 cm. long, 2-5 cm. wide, abruptly acuminate at apex with an obtuse triangular tip, subacute at base, entire or with a few minute teeth, glabrous or very sparingly stellate-pubescent above, glabrous or stellate-hirsutulous on the nerves beneath; peduncles stout, 4-10 cm. long; corymbs ebracteate, 6-10 cm. wide, 5-7-rayed, 2- or 3-times branched, densely or sparingly stellate-hirsutulous, bracteolate with minute deciduous linear bractlets; calyx tube 1.6-2 mm. long, glabrous, very sparingly glandular-punctate, the lobes triangular, slightly ciliate towards apex; corolla white, about 1.8 mm. in diameter at base, 3.8 mm. long, the lobes

ovate, rounded, 2.5 mm. wide; ovary slightly furrowed; fruit black.

Type, *Killip & Smith 16743*, collected Jan. 6, 1927, in the Río Surata Valley, above Surata, Dept. Santander, Colombia, alt. 2000-2300 m., and deposited in the herbarium of the New York Botanical Garden. Duplicates A, G, N. Other collections are: Santander: Mountains east of Las Vegas, 3200 m., *Killip & Smith 15864* (A, G, N, Y). Quebrada de País, north of La Baja, 3200 m., *Killip & Smith 18766* (N, Y). Dept. Cundinamarca: Bogotá, *Darce 168* (N).

7. *Viburnum fragile* sp. nov. Small tree; branchlets slender, terete, rufo-stellate-hirsutulous, at length glabrous; petioles 3-5 mm. long; leaves ovate, 4-6 cm. long, 2-3 cm. wide, abruptly acuminate at apex, rounded or acutish at base, denticulate near apex (teeth minute, salient, each terminating a distinct vein), sparsely stellate-hirtellous above, distinctly so near the margins, which are slightly revolute and give the appearance of being ciliate, beneath stellate-tomentose on nerves, otherwise glabrous; peduncles slender, 3-4 cm. long; corymbs ebracteate, up to 4 cm. wide, rufo-hirsutulous with simple or stellate hairs, 5-rayed, 2- or 3-times branched, bracteolate, the bractlets linear-spatulate, about 2 mm. long; calyx tube 1.4-1.6 mm. long, glandular-punctate, the lobes ovate, about 1.1 mm. long, acute, sparsely ciliate; corolla white, 1.4-1.6 mm. in diameter at base, about 3.7 mm. long, the lobes oblong, 2.4-2.7 mm. wide.

Type, *Rusby & Pennell 757*, collected August 3-5, 1917, at Basillas, Dept. Huila, Colombia, alt. 2100-2200 m., and deposited in the herbarium of the New York Botanical Garden.

8. *Viburnum leptophyllum* sp. nov. Slender shrub or small tree 3-6 m. high, glabrous throughout or minutely and sparingly appressed-hirtellous along the ultimate branchlets, petioles, and rays of the inflorescence; petioles up to 1 cm. long; leaves ovate or oblong-ovate, 5-12 cm. long, 2-6 cm. wide, obtuse or obtusely acuminate at apex, acute or rounded at base, entire, herbaceous, lustrous on both surfaces, the nerves slightly impressed above; peduncles stout, 4-5 cm. long; corymbs ebracteate, 6-8 rayed, 2- or 3-times branched, bracteolate, the bractlets linear, about 3 mm. long; calyx tube about 1.5 mm. long, glabrous, very sparingly glandular-punctate, the lobes ovate, about 8 mm. long, acute or obtusish, short-ciliate; corolla about 2 mm. in diameter at base, 3-3.3 mm. long, the lobes oblong, subacute, about 2.1 mm. wide; ovary slightly furrowed; fruit globose or globose-ovoid, 7-8 mm. long, 5-6 mm. wide, dark blue or black.

Type, *Killip & Smith 17055*, collected Jan. 13, 1927, vicinity of California, Dept. Santander, Colombia, alt. 2300 m., and deposited in the U. S. National Herbarium (no. 1,352,712). Duplicates A, G, Y. Other collections are: Dept Santander: California, 2300 m., *Killip & Smith 16931* (A, G, N, Y), *17059* (G, Y), *17083* (A, G, N, Y). Charta, 2400 m., *Killip & Smith 19098* (A, G, N, Y), *19226* (A, G, N, Y), *19310* (A, G, Y). Surata, 2200 m., *Killip & Smith 16628* (A, G, N). Las Vegas, 2800 m., *Killip & Smith 16083* (A, G, N, Y).

8a. *Viburnum leptophyllum venezuelense* f. nov. Leaves ovate or narrowly oblong, 3-7 cm. long, 1-3 cm. wide, thin-herbaceous, the nerves scarcely impressed; peduncles slender, 2-4 cm. long; calyx tube glandular-punctate with a few scattered short hairs; corolla 2.8-3.2 mm. long; ovary terete or slightly furrowed.

Type, *E. Pittier 91*, collected Oct. 25, 1921, in mountains near Galipán, Federal District, Venezuela, and deposited in the herbarium of the New York Botanical Garden. Duplicate N. Other collections are: VENEZUELA: Macarao, 1500 m., *Jahn 474* (N, Y). Federal District: Galipán, 1700 m., *Eggers 13575* (N); *E. Pittier 91* (N). Caracas, *Kuntze 1667* (Y); *Eggers 13229* (N); *Allart 83* (N, Y); *Pittier 7406* (N); *Curran & Haman 1125* (N). Coastal Range, *Pittier 8129* (N). Miranda: Los Teques, 1500 m., *Pittier 6486* (N). Mérida: Páramo Quirorá, 2600 m., *Jahn 884* (N). Páramo de Morro, 2800 m., *Jahn 1058* (N). Mérida, 1700 m., *Pittier 12857* (N, Y).—COLOMBIA: Santander: Mesa de los Santos, 1500 m., *Killip & Smith 15006* (A, G, N, Y), *15068* (A, G, N, Y), *15116* (A, G, N, Y).

This species appears to be confined to the mountains of north-eastern Colombia and western Venezuela. In the Venezuelan material the leaves are smaller and thinner, and the rays of the inflorescence very slender. Gradations between this and typical *V. leptophyllum* are found in the Colombian specimens from the Mesa de los Santos.

9. *Viburnum floccosum* sp. nov. Tree or shrub, 2.5-5 m. high, with terete branches and branchlets, the branchlets and rays of inflorescence densely rufo-stellate-tomentose with matted hairs; petioles 5-8 mm. long; leaves oblong or ovate-oblong, 7-12 cm. long, 3-6 cm. wide, obtuse or obtusely acuminate at apex, rounded at base, coriaceous, sparingly stellate-pubescent on nerves and veins; peduncles very stout, up to 8 cm. long; corymbs

ebracteate, about 10 cm. wide, 7-10-rayed (rays nearly straight, ascending), 2- or 3-times branched, bracteolate, the bractlets about 1.5 mm. long, soon deciduous; calyx tube 1.3 mm. long, glandular-punctate, the lobes ovate, .7-.8 mm. long, acutish, ciliate (cilia up to .3 mm. long); corolla white, about 2 mm. in diameter at base, 4 mm. long, the lobes oblong, about 2.2 mm. wide.

Type, *Killip & Smith 18082*, collected Jan. 24, 1927, in oak forest, vicinity of La Baja, Dept. Santander, Colombia, alt. 3500 m., and deposited in the U. S. National Herbarium (no. 1,353,553). Duplicates A, G, Y. Other specimens are: Dept. Santander: California, 3000 m., *Killip & Smith 16916* (A, G, N, Y). Charta, 2000 m., *Killip & Smith 18869* (A, G, N, Y).

10. *VIBURNUM DIVARICATUM* Benth. Pl. Hartw. 132. 1844. Shrub, 2.5-4 m. high, with lax, densely stellate-pubescent branchlets, the upper internodes 5-8 cm. long; petioles 5-10 mm. long; leaves ovate-elliptic or oblong, 6-8 cm. long, 2-4 cm. wide, acuminate or subobtuse and short-cuspidate at apex, rounded or acutish at base, subentire, sparsely stellate-pubescent on both sides, the nerves 4 or 5 to a side, relatively distant; peduncles 6-8 cm. long, somewhat curved, densely stellate-pubescent; corymbs ebracteate, up to 10 cm. wide at anthesis (broader in fruit), 2- or 3-times branched, about 7-rayed, the rays slender, wide-spreading, the flowers not clustered, distinctly pediceled, with 2 minute sessile, setaceous bractlets at base; fruit oblong, 4-5 mm. long (immature).

Ecuador: Mount Paccha (N, photo of type).

This species, known to us only from a photograph of the type, is characterized by a lax, wide-spreading inflorescence, the flowers being quite distinct from each other, even at anthesis. In this respect it resembles *V. cornifolium* (*Killip 11648*), a species with distinctly oval leaves, which have conspicuous caudate-tips.

11. *Viburnum cornifolium* sp. nov. Shrub or small tree; branchlets terete, essentially glabrous, reddish brown; petioles 4-5 mm. long, minutely appressed-hirtellous; leaves ovate or oblong-ovate, 7-14 cm. long, 4-7 cm. wide, caudate-acuminate (tip sometimes to 2.5 cm. long), subacute at base, entire, glabrous above, or usually minutely stellate-hirtellous on the midnerve, essentially glabrous beneath, the nerves 5 or 6 to a side, arcuate-ascending; peduncles 5 to 10 cm. long, minutely stellate-tomentose; corymbs ebracteate, up to 12 cm. wide, 6- or 7-rayed, 3- or 4-times branched, ebracteolate, the rays finely hirtellous; calyx tube about 1.2 mm. long, glabrous, glandular-punctate, the lobes semicircular, 0.5 mm. long, finely ciliate; corolla 1.3 mm. in diameter at base, about 2.7 mm. long, the lobes ovate, 1.8 mm. wide.

Type, *Killip 11648*, collected Sept. 24-29, 1922, at Pavas, Dept. El Valle, Colombia, alt. 1700-2100 m., and deposited in the U. S. National Herbarium (no. 1,143,262). Duplicate Y. Other collections (also from Colombia) are: Dept. Antioquia: Valparaiso, vicinity of Medellín, *Toro 1377* (Y), with larger flowers, the corolla up to 3.5 mm. long, the lobes proportionately broader, 2.3 mm. wide. El Valle: Calima, *Killip 11206* (N, Y).

12. *Viburnum Lehmannii* sp. nov. Shrub or tree (?); branchlets terete, densely hirsutulous; petioles 5-8 mm. long; leaves oblong-lanceolate, 5-10 cm. long, 2-4 cm. wide, acuminate at apex, rounded at base, entire, glabrous or sparsely stellate-pubescent above, sparingly stellate-hirsutulous beneath, the nerves 4 or 5 to a side, arcuate-ascending; peduncles 2-6 cm. long; corymbs 3-5 cm. wide, rufo-hirsutulous with simple or stellate hairs, bracteate (bracts linear, about 7 mm. long, deciduous), 6- or 7-rayed, 3-times branched, bracteolate, the bractlets linear-spatulate, 2-3 mm. long; calyx tube about 1 mm. long, glandular-punctate, with a few scattered slender hairs, the lobes ovate, about .6 mm. long, acutish, sometimes slightly ciliate; corolla 1.3 mm. in diameter at base, about 2.5 mm. long, the lobes oblong, 1.6 mm. wide.

Type, *Lehmann BT671*, collected Feb., 1884, in highlands of Popayán, Dept. El Cauca, Colombia, alt. 1500-2000 m., and deposited in the herbarium of the New York Botanical Garden. Duplicate N. Another specimen is: El Cauca: Silvia, north of Popayán, *Lehmann 969* (Y).

13. *Viburnum Toronis* sp. nov. Tree or shrub; branchlets terete, essentially glabrous, lustrous; petioles 3-5 mm. long; leaves narrowly oblong, 10-17 cm. long, 3.5-5.5 cm. wide, long-acuminate at apex (tip 1-1.5 cm. long), subacute at base, entire or subentire, glabrous above or the midnerve often minutely tomentellous, glabrous beneath; peduncles stout, 7 cm. long; corymbs ebracteate, wide-spreading, up to 13 cm. wide, 6-rayed, bracteolate, the bractlets ovate-lanceolate, up to 3 mm. long; calyx 4- or 5- times branched, the branches finely stellate-to mentulose, tube .8 mm. long, sparsely glandular-punctate, the lobes ovate, about .8 mm. long, acutish, faintly ciliate; corolla 1-1.3 mm. in diameter at base, about 2 mm. long, the lobes oblong, 1.6 mm. wide.

Type, *Toro 424*, collected Aug. 20, 1927, at Medellín, Dept. Antioquia, Colombia, and deposited in the herbarium of the New York Botanical Garden. Duplicate N.

INDEX TO AMERICAN BOTANICAL LITERATURE

1926-1929

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Studies on the morphology of Onagraceae

I. The megagametophyte of *Hartmannia tetraptera*

DONALD A. JOHANSEN

(WITH A TEXT FIGURE AND PLATE II)

In his memorable paper on the embryo sac of angiosperms Guignard (1882) includes, among other species, *Oenothera tetraptera* Cavanilles [= *Hartmannia tetraptera* (Cav.) Small]. He outlines megagametogenesis in this species, and describes the mature megagametophyte as being similar in organization to the usual octonucleate type. For some unfathomable reason, this paper of Guignard's appears to have been overlooked by most of those who have worked upon the onagracean megagametophyte; at least, attention has not hitherto been directed to the fact that if a species belonging to the Onagraceae (excluding the genera *Trapa* and *Montinia*) actually possesses an octonucleate megagametophyte, this information would be decidedly interesting, if not startling, since one of the indisputable diagnostic characters of the family is the tetranucleate megagametophyte described by all other investigators since Hofmeister (1847).

Material of *Hartmannia tetraptera* being available since 1925 in my collection of the Onagraceae growing at Stanford University, it was considered desirable to re-examine this species and to confirm or disprove Guignard's observations.

Apart from the connection between this study and that of Guignard, many interesting peculiarities were observed in the ovule and associated structures and these alone were considered of sufficient interest to warrant publication.

MATERIALS AND METHODS

It will naturally be necessary to accept for granted that the species employed in this study is identical with that of Guignard, since the latter neither describes his species in any particular nor states the source of his plants. Certain historical information, however, is available. From Desfontaines (1829) we learn that as early as 1804 *Oenothera tetraptera* was cultivated in the garden of the Museum d'Histoire Naturelle in Paris and that the original source of the species is given as Mexico. *Oenothera rosea* was also cultivated, its country of origin being Peru. Curtis (1800)

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gives the native country of *Oe. tetraptera* as Mexico, adding that it was probably first introduced into England from Spain. Curtis' illustration is quite accurate, but in my plants I have never noticed the red spots on the stems and the reddish margins of the older leaves which his figure shows.

The geographical range of *Hartmannia tetraptera* is from Texas through Mexico and Central America to northern South America. It occurs also in Jamaica. It has so far been impossible to collect material from plants in their native habitat, hence recourse to cultivated plants became necessary. Live plants were secured from Mr. Carl Purdy of Ukiah, California, and seed from Heinr. Mette of Quedlinberg, Germany. In the garden only minor genetical differences were observed from 1925 to 1927, but these became more pronounced in 1928.

Purdy's plants are doubtless Texan in origin, but those grown from the German seed probably came originally from Mexico, perhaps by way of France. An examination of herbarium specimens at the New York Botanical Garden gave evidence that as one progresses northward from the Mexican plateaus into the Texan plains, the plants become larger, the foliage less dissected below, and the flowers become larger and usually take on a reddish tinge, even becoming rose-purple in color. The flowers of my plants were pure white in color, turning pinkish on dying.

H. tetraptera has been much confused with *H. speciosa* and even more so with *H. rosea*. Many of the plants circulating among gardeners as *H. rosea* are probably only rose-flowered varieties or forms of *H. tetraptera*. There is also considerable confusion regarding the plant variously known as *Oenothera mexicana rosea*, *Oe. rosea mexicana*, *Oe. Childsii* (Child's Evening Primrose) etc. This plant is identified by Bailey (1916, p. 2332) as *Oe. tetraptera* var. *Childsii*. It is distinctly a *Hartmannia* and in my garden is labelled *H. tetraptera* var. *Childsii*, it being intended that this combination shall stand until further research establishes the true status of the species. I am inclined, as is Bailey, to consider it a distinct species.

Young ovaries to illustrate the series of stages comprising megagametogenesis were trimmed down to a convenient size, placed in Petrunkewitsch's fluid, and the air removed with a special hand pump. For later stages, beginning with fertilization,

it is necessary to cut away all ovarian tissue possible. For the early stages in embryogenesis fixation in a modified formalin-acetic acid-alcohol was more satisfactory. The ovaries were sectioned both transversely and longitudinally at 12 microns, and stained with safranin, counterstained anilin blue (for permanency) or light green (somewhat fugitive on this material).

HISTORICAL RÉSUMÉ

Gates (1928) has recently given a résumé of studies on the embryo sac of the Onagraceae, hence it will merely be necessary to mention certain omissions in his summary. In addition to Guignard's paper, Gates has omitted those of Vesque (1879), Rutgers (1923) and O'Neal (1923); he fails to note that certain authors whose papers are mentioned under other headings have given attention to various details of megagametogenesis (e.g. Håkansson, 1924).

Since it is now known that nuclear behavior in most of the *Fuchsias* is irregular (vide Täckholm, 1915, Johansen, 1927), and in view of the notorious prevalence of parthenocarpy in the genus, it is not at all surprising that Vesque describes anomalous stages leading up to the organization of a pentanucleate megagametophyte in *Fuchsia fulgens*. His observations lose some of their quality through lack of comparison with species in related genera. Rutgers includes the Onagraceae in his study of the female gametophyte of angiosperms but makes no new morphological contribution. O'Neal describes the development of the megagametophyte and fertilization in *Oenothera rubrinervis*. The writer (Johansen, 1927) has described various stages in the development of the megagametophyte of nine Californian species.

THE OVARY AND OVULES

Although the earlier stages in the development of the ovule were not followed out in detail, there is nothing to indicate any irregularities which might later affect the organization of the megagametophyte. At the time the gametophytes are ready for fertilization, the ovary contains a large number of ovules loosely and variously arranged in each of the four locules. Some ovules are parallel to the locular wall, others are horizontally placed, while still others are reversed from the normal anatropous posi-

tion typical of the Onagraceae. Every degree of variation between the extremes is to be seen. The first meiotic mitosis occurs more or less simultaneously among all the ovules, but after that the ovules do not all develop at the same rate, consequently only a small percentage of the gametophytes are at the same stage of development or organization.

The partitions separating the locules disintegrate at an early stage, thus giving the numerous ovules more room in which to expand. The ovules, nevertheless, are among the smallest in the family and are characterized by the compactness of the various ovular structures.

Twin ovules occur frequently. They are enclosed in a common inner and outer integument and are ordinarily separated by distinct nucellar epidermal layers, though in a few instances a modified inner integument separates the two. Each twin possesses its individual hypostase. No attempt has ever been made—at least, not in this species—to ascertain the origin of these twin ovules.

This species possesses a very prominent hypostase (fig. 13), which often appears to assume the cupule form originally described by Van Tieghem (for a discussion of this subject and the pertinent literature, see Johansen, 1928). This condition is brought about when the characteristic fluid substance filling the cells comprising the hypostase permeates the inner layer of the inner integument (one layer of cells in thickness), beginning at the chalaza and extending to the apex of the ovule, where an epistase independently makes its appearance shortly after fertilization.

DEVELOPMENT AND ORGANIZATION OF THE MEGAGAMETOPHYTE

a) *The megasporocyte.* In *Hartmannia tetraptera* the megasporocyte does not make its appearance in the ovule at the early stage that it does in many other onagrad; the reason may possibly be found in the fact that early growth of the ovule is comparatively slow. A large hypodermal cell at the apex of the nucellus becomes larger than its fellows, shows evidence of greater metabolic activity, and is soon identifiable as the archesporial initial. It divides periclinally, the lower daughter cell becoming the megasporocyte, whilst the upper, by a succession of principally periclinal divisions, gives rise to a regular series of cell-layers be-

tween the micropyle and embryo sac (the tapetum). These divisions rapidly place the elongating megasporocyte deep in a large mass of cells, directly over the chalazal end of the ovule. There is, in this species, not the wide variation in number of layers of tapetal cells found in many other onagrads. The megasporocyte gradually increases in size, especially in length, and the nucleus moves slightly towards the micropylar end. The lower part of the cell is occasionally occupied by a vacuole, brought into existence by reason of the fact that the cytoplasm does not increase at the same rate as the cell, but it presently disappears. Preparation for the meiotic mitoses resulting in the formation of the quartet now commences. Only one megasporocyte has ever been observed in this species; it might be said in passing that I am constrained to regard with skepticism some of the published accounts of 'several archesporial cells' in various onagrads: in the earlier stages of the present work my notes read 'probably several archesporial initials,' but the fact that only a single mature megasporocyte was ever observed led to critical attention being devoted to this topic. With carefully controlled staining it was demonstrated that cells adjoining the archesporial initial may often simulate the functional appearance of the latter.

b) Meiosis. Since this paper is primarily morphological, it is not intended to enter into a detailed discussion of meiosis; this topic will be treated in a later paper in connection with a discussion of meiotic phenomena in the microsporocyte. However, it may be stated that the mode of meiosis is telosynaptic and that the normal haploid number of chromosomes is seven, the diploid fourteen (fig. 1). Variations in the number of microsporocytic chromosomes (seven, eight, ten) have been found in 1928 material; the range has not yet been determined.

c) The quartet. The reduction divisions result in the formation of four megaspores, arranged in a linear series. In so far as potentialities for germination are concerned, each megaspore is equal to the others, but the micropylar megaspore of the quartet invariably becomes functional. The three inner megaspores persist for a long time, and may even be observable after fertilization has taken place (figs. 2, 3).

d) The megagametophyte. During the growth of the functional megaspore, a gradually enlarging vacuole appears in the

chalazal portion, forcing the nucleus towards the other end of the cell (fig. 2). The size of the vacuole varies considerably, but the nucleus is always to be found near the micropylar end of the cell. When the new megagametophyte, now in the initial stages of organization, has about attained its limit of expansion, the first division occurs. The plane of the spindle of this division is always parallel to the longitudinal axis of the ovule. The binucleate condition persists for some time, during which period the sac enlarges a little more at the expense of the surrounding nucellar cells. In the second and final division, the plane of the spindle of the upper (micropylar) nucleus is transverse, while that of the lower is parallel to the longitudinal axis (fig. 3). There are two divisions only in the functional megaspore of the Onagraceae, in contrast to the three which give rise to the octonucleate gametophyte in the majority of angiosperms.

The organization of the four free nuclei into the various structures of the mature megagametophyte has not been described in detail for any onagrad, probably because the process, when once initiated, is consummated with incredible rapidity. My own observations are not as thorough as might be desirable, but they are perhaps worth recording. The two nuclei derived from the nucleus remaining in the upper portion of the sac following the second division become the synergid nuclei, while those from the lower nucleus become respectively the nucleus of the egg cell and the polar nucleus. The spindle fibers from the division of the uppermost nucleus initiate the formation of the walls surrounding the two synergids, while the lower spindle disappears immediately upon the reorganization of the daughter nuclei (fig. 4). The two walls being formed are loosely held together and are not connected by a middle lamella; this permits divergence of the walls and the assumption of the pyriform shape of the synergids. It has been very difficult to establish the exact manner in which the egg cell wall arises, if one prefers to seek a mechanical explanation rather than accept the alternative theory that it originates *de novo* in the cytoplasm. The only objection to this alternative is that it does not explain why a wall is not also formed around the polar nucleus. In the lower part of the diverged synergid walls an unequal split was thrice observed. This constitutes the basis for my theory that the egg cell wall, if not an outgrowth from those

enclosing the synergids, is at least stimulated into development by and during their growth. Its origin is diagrammatically explained in text-figure 1. It differs from the synergid walls in that the latter give cellulose reactions alone, while the egg cell wall has neither a pectic nor a cellulose reaction. The latter reactions were also obtained by Ishikawa (1918). Cell walls in abnormal embryo sacs are usually simple protoplasmic membranes.

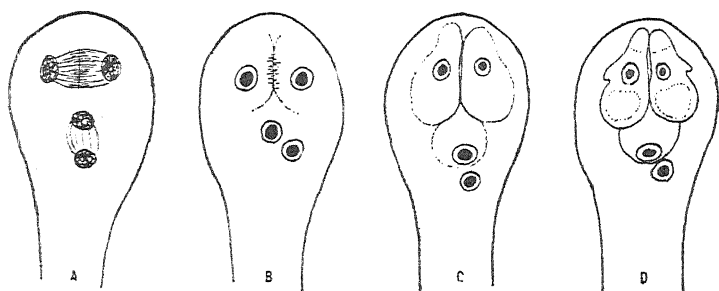


Fig. 1, A-D. Wall formation in the megagametophyte of the Onagraceae, based on *Hartmannia tetraptera* (diagrammatic). (A) Conclusion of the second and final division in the embryo sac. (B) Early wall formation. Notice the disappearance of the lower spindle. (C) Later stage. Wall between the synergids is definite; elsewhere it is still in a formative stage. (D) Wall formation complete; megagametophyte mature and ready for fertilization. The splits in (C) are due to the fact that no middle lamella is developed.

The egg cell is more or less open towards the apex; the nucleus together with a small amount of dense cytoplasm is crowded against the lower wall by a huge vacuole which occupies by far the greater part of the egg cell (figs. 8, 10).

The polar nucleus in about half the observed cases is non-nucleolate, a rare condition for the family. In many instances of nucleolate polar nuclei, the nucleolus has a distinctly amoeboid shape. This phenomenon has been observed in other species, and is considered a stage in the decreasing importance of the 'endosperm.' This topic is being discussed in detail in another paper of the present series.

In *H. tetraptera* the developing megagametophyte attacks the surrounding nucellar cells to a greater extent perhaps than in any other species of the family so far investigated. The female

gametophyte is always broad and densely packed with foodstuffs, hence the unusual ravages upon the nucellar cells may be explained. The starch grains are large in size but sparingly scattered throughout the entire tapetum and in the greater portion of the nucellus. However, the mass of the demolished synergids together with the remnants of the pollen tube provides the main source of nutriment during the earlier stages of embryo development.

c) *The filiform apparatus and synergid indentations.* This paper was ready to be forwarded for publication when the paper of Dahlgren (1928) on synergid indentations appeared. Since my conclusions are different from Dahlgren's, and a somewhat more comprehensive series of observations have been made, it was felt advisable to reconstruct and enlarge those portions of the paper relating to these topics.

Normal megagametophytes of *H. tetraptera* have been roughly divided into two classes, although the ultimate significance of the basis for the division cannot be foretold. The first class (fig 7) is characterized by the presence of the peculiar filiform apparatus in the beaks of the synergids, while in the other group (fig. 6) there is no indication whatever of this peculiarity. In other structural details the two classes are essentially similar, and they occur in approximately equal numbers in any given ovary.

Dahlgren does not devote any particular attention to the filiform apparatus, merely quoting the opinion of one writer that the formation of indentations depends upon the existence of the filiform apparatus, and quoting the converse for another writer. The median course seems preferable, since there is no indisputable evidence that a definite relationship exists between the filiform apparatus and the indentations.

The filiform apparatus, when present, is a semi-solid mass in whose lower portion are found a number of very minute canals or striations, arising in the basal part and converging towards the apex, but not reaching the tips of the synergids (fig. 7). This structure, as noted by Dahlgren, has been found in a great many plants from other families, but my observations indicate that it is especially prominent in, and characteristic of the Onagraceae. It is readily revealed by light green used in contrast to safranin, though gentian violet is more likely to indicate the delicate pores

or striations. The uppermost part of the synergid, above the striations, is a clear space, which is doubtless the repository for the chemotactic substance supposed to attract the microgametophyte. Dahlgren, however, believes that the evidence that the synergids secrete a chemotactic substance is based on 'rather loose grounds.' I do not concur in this view, for in *Clarkia elegans* I have often noticed on the external walls at the tips of the synergids large droplets of an exudate which have the identical chemical reactions of the substance contained in the apices of the synergids. Smaller droplets may even be found in the tapetum where the cells have broken apart. It appears more likely that this substance secreted by the synergids does not necessarily of itself act chemotactically towards the microgametophyte, but assists in preparing the way for the entrance of the latter by attacking the cells in the tapetum between the micropyle and the apex of the embryo sac. In those synergids lacking the filiform apparatus, the apices contain the same finely vacuolate cytoplasm as is found in other parts of the synergid outside the basal vacuole (fig. 6).

In his earlier work, Dahlgren considered the indentations to be artifacts, but later modified this view, and wrote: 'If the indentations are not attributable to methods of preparation, their origin must be dependent upon developmental-mechanical causes alone.' He believes with Asplund that they are 'certainly without any physiological significance.' To summarize my own conclusions regarding the indentations peculiar to the onagrad synergids: they are as perfectly natural characters as the filiform apparatus or the omnipresent basal vacuole, and their purpose may be both physiological and mechanical. It should be borne in mind that synergids which become haustorial, as in *Helianthus annuus* and in many other Compositae, are in an entirely different category from synergids which are prevented by comparatively thick cellulose walls from becoming haustorial. Haustorial synergids, moreover, rarely if ever possess the filiform apparatus; in such synergids, physiologically speaking, the haustorial function supplants the 'chemotactic' and to the same end.

Synergids possessing a well defined filiform apparatus apparently have a high metabolic rate, and as they become older they get more and more exhausted, since they cannot receive from

outside the equivalent of 'raw materials.' Collapse and shrinkage are inevitable unless fertilization intervenes; this is especially true of species inhabiting localities that support herbaceous plant life for two or three months only per annum. The shrinkage of synergids has no connection whatever with the presence or absence of indentations. The indentations, which extend around approximately three-fourths the circumference of the synergids, are clearly shown in text-figure 1, *D*.

The synergids have been observed to serve a definite mechanical purpose. In megagametophytes whose synergids very likely lacked indentations, the microgametophyte entered with such force that both synergids were completely demolished and the egg cell was forced beyond the center of the sac. In other species whose synergids were supplied with well formed indentations, the initial force seemed to be the same as in *H. tetraptera*, but the synergids withstood the shock without much damage to themselves. These facts furnish the basis for the writer's theory that one of the principal functions of the synergids is to serve as 'shock absorbers' against the too violent entrance of the pollen tube, thus preventing the complete demolition and consequent degeneration of the megagametophyte.

Dahlgren states that he investigated plants of the Onagraceae but found unmistakable indentations in *Clarkia pulchella* only. *Clarkia*, *Eucharidium* and *Godetia*, I find, are very likely to have shrunken synergids because ovaries of these genera are very difficult to fix properly. The *Epilobiums* have very poorly developed synergids. In other onagrad, beautifully organized synergids may easily be found in *Anogra trichocalyx*, *Sphaerostigma Veitchianum*, and *Zauschneria californica*.

TERATOLOGICAL MEGAGAMETOPHYTES

Many types of irregularities are frequently met with (figs. 9, 10, 11, 12), and poor organization of the megagametophyte is commonly encountered. The trouble generally lies with the primary synergid nucleus, which often fails entirely to divide; sometimes it simulates the appearance of a normal (i.e. for this species) synergid (fig. 10), and in other cases it is merely a large cell (fig. 9). In any event, it may be identified by the omnipresent basal vacuole. This recalls conditions in the markedly anomalous

megagametophytes of the garden Fuchsias. The failure of the primary synergid nucleus to divide disrupts the organization of the gametophyte; but despite the lack of normality, few supernumerary nuclei and no superfluous sacs have been observed in the hundreds of ovaries sectioned and examined.

CONCLUSIONS

In conclusion, the megagametophyte of *Hartmannia tetraptera* may be considered a pronouncedly transitory type, and this is in agreement with the idea of Broekens (1924) that the genus (= *Xylopleurum*) constitutes an intermediary group between *Kneiffia linifolia* and *Jussieuia*-like ancestors. The only species of *Kneiffia* of which I have preparations available at present is *K. fruticosa* (incl. *K. linearis*), originally obtained in 1925 from Mr. Purdy's nursery. I cannot tell how closely it resembles *K. linifolia* morphologically. The synergids of *K. fruticosa*, in the majority of mature megagametophytes, possess well defined indentations, while in others this peculiarity is somewhat rudimentary. The filiform apparatus is always present.

The evidence seems conclusive that Guignard was somewhat hasty in his attempt to substantiate his thesis that the embryo sacs of all angiosperms have the same fundamental octonucleate organization. Either his observations were incomplete or his interpretations erroneous; the only explanation possible is that his two polar nuclei represent a binucleolate polar nucleus and the three 'poorly developed antipodals' are the three persistent, non-functional megaspores (consult fig. 3). The synergids and egg cell as delineated require no special criticism.

SUMMARY

1. Guignard's description of an octonucleate megagametophyte for *Hartmannia (Oenothera) tetraptera* is not confirmed: the species is as regularly tetranucleate as any other species of the Onagraceae.
2. The species is in a transitory stage, as evidenced by cytological behavior in the megaspores, megagametophytes and microsporocytes. Phylogenetic forces are in active operation.
3. The probable method of cell-wall formation in the embryo sac is described.

4. The filiform apparatus and the indentations characterizing the synergids are entirely normal structures.

5. The normal haploid number of chromosomes is 7, the diploid 14, but some variation exists.

The material was collected while the writer was a University Fellow at Stanford University; the paper was prepared during the tenure of a National Research Fellowship in the Biological Sciences, with residence at the New York Botanical Garden.

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Description of plate 11

All except figure 13, $\times 450$. Figure 13, $\times 100$.

Fig. 1. First meiotic mitosis in the megasporocyte. Seven haploid chromosomes.

Fig. 2. Binucleate megagametophyte. The lower three megaspores still persistent.

Fig. 3. Second mitosis in the megagametophyte. Seven haploid chromosomes on each spindle. In this instance, the three non-functional megaspores are *within* the embryo sac, the cytoplasm of one having partially united with that of the megagametophyte. It was doubtless in a case such as this that Guignard mistook the non-functional megaspores for antipodal cells.

Fig. 4. Tetranucleate megagametophyte, with the earliest observed stage in the process of synergid wall development.

Fig. 5. Organization of the megagametophyte nearly complete. The characteristic vacuole is just appearing in the synergid to the left.

Fig. 6. Mature megagametophyte representing the type characterized by the absence of the filiform apparatus.

Fig. 7. The same, but with the filiform apparatus present. In this, as in the preceding figure, the indentations are absent from the synergids. The polar nucleus in each case is non-nucleolate.

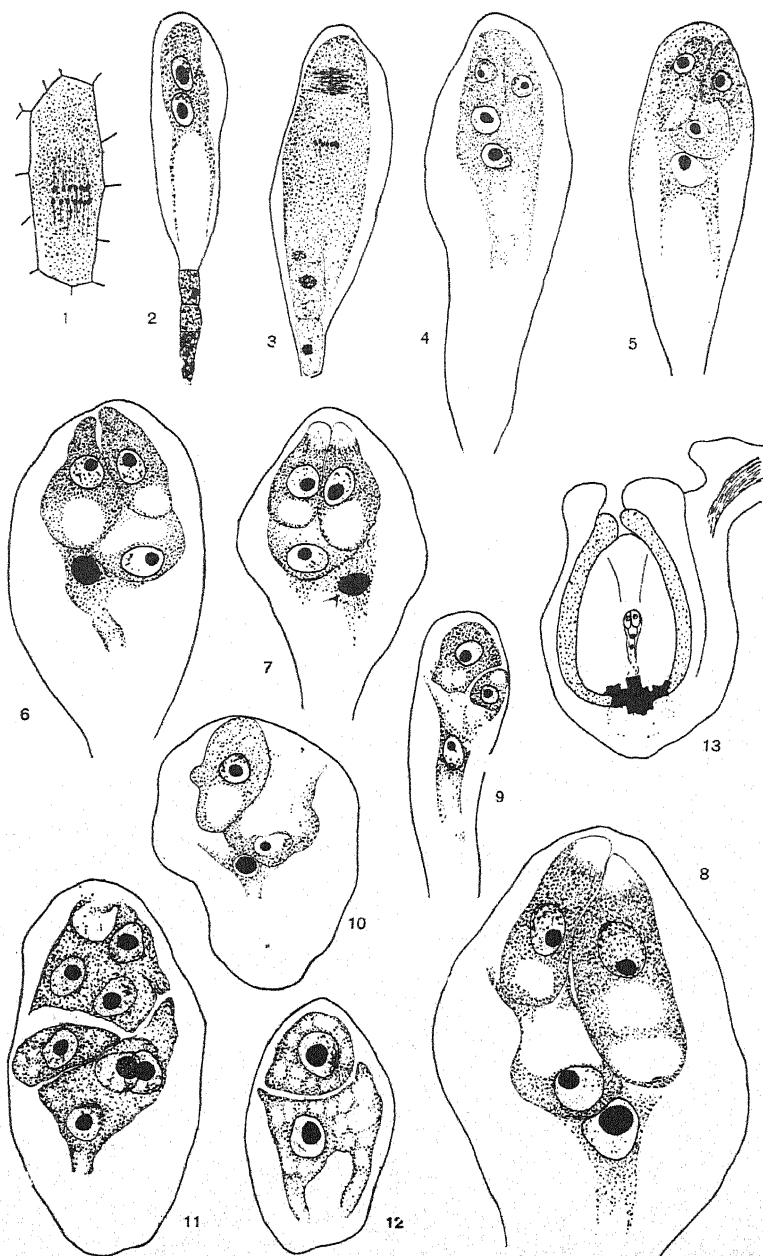
Fig. 8. Hypertrophied synergid in an unusually large embryo sac. Polar nucleus is nucleolate.

Figs. 9, 10. Abnormal megagametophytes in which the primary synergid nucleus failed to divide. The synergid in figure 10 has a double indentation.

Fig. 11. An abortive attempt to form two megagametophytes in the same embryo sac. The fourth nucleus of the upper group is in a succeeding section.

Fig. 12. Probably an earlier stage than the preceding figure. The cause seems to lie in a precocious mitosis in the functioning megaspore, with simultaneous transverse cleavage of the cytoplasm.

Fig. 13. Topography of the ovule (median longitudinal section) at the time the megagametophyte is ready for fertilization. Inner integument stippled; hypostase solid black.



A comparison of the behavior of crown gall and cancer transplants

MICHAEL LEVINE

(WITH PLATES 12, 13)

The transfer of small pieces of tumor tissue from one animal to another of the same species is now a well established laboratory procedure for propagating animal cancer. The view held by Jensen (1903) and confirmed by Bashford and Murray in 1904, and together with Cramer in 1905, that the growth of the transplanted portion of the tumor is responsible for the new growth in the host and is not the product of the host, is now also generally accepted (see Loeb, 1901-2).

A study of the transplanted malignant cells shows that they possess the faculty of continuous growth and utilize the tissue of the host to the fullest extent. The host tissue does not acquire the power to proliferate.

The stroma of the tumor, however, consists of a connective tissue network and a blood supply system which are the direct outgrowths of the host. The stroma forms the framework about which the rapidly dividing and growing cancer cells are formed. This reaction of the host Ehrlich (1907) attributed to specific substances formed by the tumor cells which act upon the fibroblasts and angioblasts of the host. Apolant, according to Woglom (1913) believes that the preponderance of one of these elements of the stroma over the other is due to an unequal stimulation of the *Anlagen* of these tissues. A well balanced stimulation of both elements produces a well supported and well nourished carcinoma. Gierke (1908) pointed out that the extent to which a cancerous growth develops depends upon the formation of the connective tissue and blood vessels. The character of the blood supply furnished by the host may be altered by changes in temperature. Certain hosts which are resistant to the growth of the transplant fail to produce the necessary blood supply for it.

Crown gall is a localized overgrowth of plant tissue and may be induced most readily by pricking the plant, where the plant tumor is desired, with a steel needle previously immersed in a sub-culture of *Bacterium tumefaciens*. The inoculation of this organism, preferably into the younger portions of the plant,

results in the development of an overgrowth of tissue in the region of inoculation from fifteen to thirty days later. The development of fibrovascular elements in plant overgrowths has been considered by Smith (1911) as analogous to the stroma in animal cancer.

This so-called stroma of the crown gall tissue presents a marked contrast to that in animal or human cancer. The young tumor in plants shows no fibrovascular elements. In old crown galls the fibrovascular elements, if present, may be due to the displacement of old tubes and vessels by the growth of the rapidly proliferating meristematic tissue formed about them, or they may arise, as they most frequently do, by the differentiation of the proliferating cambium tissue. In this case nourishment could hardly be brought through the disconnected and isolated vessels or tubes. These vessels or tubes arise entirely from the crown gall tissue itself and do not grow into the gall. In the former cases the crown gall tissue surrounds the old fibrovascular elements. These elements are not capable of further growth once they are fully developed.

The transplantation of crown gall tissue to healthy parts of the same plant (autotransplant) or to other plants (homeo- or heterotransplants) has never been a question of the propagation of this disease. The transplantability of crown gall tissue to healthy plants is another means of comparing the proliferating power of crown gall and cancer cells, and of establishing any analogy that may exist between them.

Jensen (1910, 1918) compared the neoplasms of animals and plants, and raised the question of the transmissibility of this plant disease by transplants. He transplanted inocula of crown gall tissue of spontaneous and artificially produced origins to healthy plants of the same species. Jensen (1918) figures the results of successful transplantations of crown gall tissue from the yellow sugar beet to the red mangel, and of the crown gall tissue of the latter to healthy roots of the former. He contends that the tumors formed are due exclusively to the growth of the transplanted crown gall tissue, which corresponds in appearance and structure entirely to the mother tumor. It is of importance to note that isolation of *B. tumefaciens* from the spontaneous crown galls of mangels and sugar beets was suc-

cessful in only one case. Jensen believes that while *B. tumefaciens* causes crown gall in beets, the bacteria die off in older plant overgrowths. He was unable to recover this organism from crown galls produced by transplanted tissue of spontaneous origin. Jensen thinks it extremely probable that the cells of the tissue under the influence of the bacteria become altered for a series of generations and develop the increased proliferating power which becomes independent of continued stimulation. Jensen states that tumors on beets produced artificially through the agency of *B. tumefaciens* behave like spontaneous growths. Jensen obtained the same results with his transplants whether he used spontaneous or artificially produced tumors. On the basis of these observations Jensen holds to the opinion that crown gall is analogous to animal cancer.

In view of these results it has seemed to me to be of interest to study further the transplantability of artificially produced crown galls and their effects on the host of similar species. Another point of interest is to test the effect of crown gall tissue of one species of plant transplanted on widely separated species. The production of crown gall disease under these conditions would tend to indicate that this is an effect of the bacterial organism present in the transplant rather than the growth of the inoculum. Spontaneous crown galls, according to Jensen, have few or no bacteria, while artificially produced crown galls in my studies yield an abundance of *B. tumefaciens* under proper cultural conditions. It has been shown (Levine, 1923) that the number of bacteria introduced into a wound in the plant is of no importance in the production of the overgrowth.

It is with crown gall of the artificially produced type that my tests were made in order to throw further light on the question of the behavior of crown gall transplants and their analogy to transplants of animal cancer.

MATERIAL AND METHODS

Experiments on the transplantability of crown gall tissue to healthy plants were started in the spring of 1925 and were carried on for three consecutive summers. Most of the tests were repeated two and three times. The plants studied were

grown in the garden. A large number of the experiments were carried over the winter season in the greenhouse and in a well lighted room. The garden space was divided into a number of plots, each of which was sown with seeds or cuttings of one species of plant. The castor bean (*Ricinus communis*), tomato (*Lycopersicum esculentum*) var. earliana, and the beet (*Beta vulgaris*) vars. garden beet, yellow tankard, and red colossal were the chief sources of crown gall tissue as well as hosts for the transplants. The geranium, tobacco (*Nicotiana affinis* and *N. Tabacum*), the rubber tree (*Ficus elastica*) and the rose plant were used primarily as hosts.

Some of the plants in each plot were inoculated with young or old sub-cultures of a virulent strain of *B. tumefaciens*. Only young petioles and growing points of the plant were used for study. Crown galls were formed in all plants by the inoculation of the bacterium fifteen or thirty days later. *N. affinis* in my cultures failed to yield crown galls on inoculation with this organism. These plants remained immune to crown gall throughout this experiment. In 1928 over 200 inoculations were made with *B. tumefaciens* in over 100 plants of this species without producing any overgrowth.

Young crown galls used for inoculation purposes were removed together with a larger portion of the plant on which they were growing. The shoot, root, or leaf was taken to the laboratory, where the crown gall was removed with a sterile knife and forceps. The gall was washed several times in sterile water and was then subjected to a weak solution of bichloride of mercury for several minutes. The entire gall was again washed in sterile distilled water. The crown gall was then cut into wedge-shaped fragments, the greatest measurement of which was about 1 mm. to 3 mm. These were placed in a sterile Petri dish and were then introduced into the tissue of the healthy plants. A small wedge-shaped incision was made in the host plant and the inoculum was introduced so that the outer surface lay inside of the surface of the host. An inoculum larger than the size of the incision was selected so that gentle pressure was required to make the host tissue hold the inoculum in place. In a few cases two or three turns of a light-weight cheese cloth were placed about the host over the region

of the inoculation. In the case of the beet transplants, the root was uncovered for a short distance below the crown and the inoculum was introduced into the incision made there. There appeared to be no marked difference in the result obtained whether the upper part of the root was covered again with soil or remained exposed. The covered roots were subject more often to worm infections.

Crown gall tissue of the castor bean was transplanted to the same plant (autotransplant), to other castor bean plants (homeotransplant), and to other plants of different genera such as the tomato, geranium, rubber plant, and garden beet (heterotransplant). Crown galls of the tomato were studied in the same way. The crown gall of the yellow tankard mangel was transplanted to the red colossal mangel and the common garden beet. The crown gall of the latter was transferred to the roots of the first. Crown gall tissue of the beet induced by *B. tumefaciens* inoculations was also tested on the castor bean, tobacco, and tomato plants.

Control studies were made on the same plants that received crown gall inocula. The control tissue used consisted of small fragments of young petioles or growing points free from crown gall tissue or *B. tumefaciens*. All the plants were carefully labeled at the region where the inoculation of the tissue was made. Crown galls produced by crown gall transplants were used again for inoculating purposes in a manner similar to that described above.

Microscopical examinations of the hosts with their transplants were made. Cultural studies were made of the organisms isolated from the crown galls used as transplants and from those derived from the transplants.

BEET CROWN GALL

Transplantable animal tumors once established may be propagated from animal to animal with considerable ease for many generations. In this case it is generally accepted that the transplanted tissue is alone responsible for the new growth. A framework of connective tissue and a blood supply is developed by the host for the new growth. The results given in this report are derived from a study of the effects of crown gall in-

ocula on the host after auto-, homeo-, and heterotransplants were made in order to determine the analogy of this plant disease to cancer in animals and man.

The chief subjects of this study were the castor bean, the common garden beet, the yellow tankard mangel, and the tomato. The tobacco, geranium, the rubber plant, and the rose plant were used as hosts. Artificial crown galls were produced by inoculating growing parts of these plants with a culture of *B. tumefaciens*.

It may be of interest to note that the color of the pigment in the crown gall of the garden beet resulting from the bacterial inoculation is a deep maroon color at the margin while the inner portions contain a yellowish-red pigment (fig. 18). The crown gall of the red colossal mangel (fig. 17) lacks pigment in the interior, while the surface is reddish in color, resembling that of a small spring radish. The crown gall on the yellow mangel presents similar variations in color. The yellow pigment is distributed over the surface of the gall and is identical in shade with the color of the normal roots. The interior of the gall is streaked with a faint yellow pigment or may be entirely lacking in pigment. It must be borne in mind that there is no sharp demarkation between the pigmented and non-pigmented areas. There is a tendency of one colored zone to blend with the other. Recognition of these color differences aids one in tracing the growth of the inoculum.

As mentioned above, pieces of crown gall tissue on the common garden beet produced artificially by the inoculation of the root with a virulent strain of *B. tumefaciens* were transplanted to eighty young roots of the yellow mangel. The greater number of these inocula failed to grow or take hold of the host or produce any overgrowth. These roots (48 in number) after three months showed normal scar tissue without evidence of crown gall formation.

In thirteen cases crown galls of the host appeared thirty days after the transplant was made. These were typical crown galls of the yellow mangel with a dense yellow pigment on the surface and pale yellow or non-pigmented tissue in the interior. In these cases the red colored inoculum from the garden beet

crown gall had disappeared or could be seen as a small shriveled and blackened body lying in the scar of the root.

In three cases undeniable growth of the transplanted garden beet crown gall occurred. The inoculum had become attached to the host tissue and developed into a gall of appreciable size as shown in figure 19. This photograph represents the root of a young yellow mangel upon which a typical garden beet crown gall has formed, cut longitudinally through the gall and the root. Here, however, one finds evidence supported by observations given below on a large number of heterotransplants that the host tissue is also involved in the formation of the growth of this tumor. Freehand sections of these roots enabled me to trace the growth of the host and the inoculum. The photograph shows clearly that the crown gall arises from the lower surface of the incision made in the host. The upper surface of the incision now appears as a dark narrow compressed band of tissue which shows no evidence of growth. The lower surface of the cut in the host has proliferated and formed part of the crown gall. Bands of faintly yellow colored tissue may be traced from the surface of the host into the grown inoculum. A microscopic examination of the tissues at above and below the region where the transplanted crown gall and host meet, as shown in figure 20, leaves no doubt as to the stimulation of the host to crown gall formation. The yellow pigmented tissue found in the crown gall of the garden beet is not to be confused with the color of the yellow mangel crown gall. While I made no analysis of these two pigments, the color differences are so striking that the one cannot be confused with the other. The major part of the crown gall in this case is shown in the photograph (fig. 19) as a deep red globular mass of tissue, while fainter red and yellow portions may be seen at the region of union of the host and transplant as indicated by the arrow. The shade of the yellow pigmented areas is typical of the color of the crown gall on the yellow mangel produced by an inoculation with *B. tumefaciens*. The passage of yellow pigment from the host into the crown gall inoculum is questionable. Hoffmann (1927) in studying reciprocal grafts of pigmented and non-pigmented bean plants finds no evidence for the movement of pigment from host to graft or the reciprocal.

Sixty roots of the garden beet and the colossal red mangel were inoculated with pieces of crown gall produced by the inoculation of *B. tumefaciens*. One root was observed in which the inoculum succeeded in establishing itself. The yellow colored gall was easily recognized. Sections of this gall showed clearly the presence of red tissue of host as evidence of its proliferation. Necrosis followed rapidly the removal of this plant from the soil so that photographic reproductions were made impossible. In eight cases in this series typical red crown galls developed after inoculating the garden beet and red mangel with crown gall tissue of the yellow tankard. The inocula in most of these roots were still to be identified although they had degenerated into very small particles of matter held firmly by the partly enveloping scar tissue. The remaining roots in this experiment showed only scars of varying size without any evidence of proliferation equal to crown gall formation.

While the number of cases cited here of successful transplants of inocula are few, the evidence is quite clear that crown galls may be produced on healthy plants by introducing pieces of crown gall tissue irrespective of the success of the transplant in establishing itself. When the transplanted crown gall tissue succeeds in establishing itself on the host, the transplant as well as the host takes part in the formation of the new crown gall. It appears that the crown gall transplant behaves like an ordinary graft for a limited time, yet, due to its inherent pathogenic properties, it is capable of further growth and also of stimulating the host to proliferation. Control studies made with sterile tissue gave scars only. The newly formed tissue of the host in successful crown gall transplants is not analogous to the stroma of the animal tumors (Levine, 1925). The fibrovascular elements found in crown gall tissue arise from the development, differentiation and aging of crown gall cells.

Heterotransplants were made in which the crown gall of the beet was inoculated into young nodes and petioles of castor bean plants. These inoculations were carefully made so as to avoid undue injury in order to secure the best advantages to the implanted tissue. The inocula were carefully watched from day to day. Light bandages were applied in a number of cases to prevent drying out of the inocula. In twenty cases studied it

was observed that the inocula grew smaller and finally dried up in spite of the protection of the cloth. However three plants in this series of experiments produced crown galls of the globular type at the bases of the scars formed. Figure 5 is a photograph of a *Ricinus* stem inoculated with a piece of garden beet crown gall. The crown gall in this picture represents the overgrowth of the host entirely, since the beet inoculum has long disappeared. Figure 6 represents a longitudinal section of the same stem. The area below the gall, indicated by the arrow, shows the region occupied by the transplant in which considerable necrosis of the tissue is to be seen.

Thirty tobacco plants (*N. affinis*) which failed to respond to inoculations with *B. tumefaciens* yielded one small questionable crown gall. The dead inocula were found in the scars of the host.

CASTOR BEAN CROWN GALL

Crown galls on the castor bean (*Ricinus communis*) produced by a culture of *B. tumefaciens* were used as transplant material. Sixty-two homeotransplants were made which yielded forty-four crown galls on as many plants. In no case was there any evidence of the proliferation of the inoculum. The transplanted inocula were so inserted into the tissue of the host that they were exposed to view, yet they were not unduly exposed to the direct light and heat of the sun. The inocula were observed to dry up in all cases in this series. A large scar was formed, due to the subsequent growth and elongation of the tissue inoculated. This was followed by the development of one or more crown galls (fig. 1) in each scar twenty to thirty days later. Twenty-five control inoculations made on petioles and stems of the same plant with healthy bits of tissue produced only callus tissue without crown gall formation (fig. 2).

A small number of autotransplants of crown gall tissue was made on the castor bean. In each case a crown gall was formed on the host without the growth of the inoculum. Second and third generation homeotransplants were made from crown galls produced by inoculating crown gall tissue. Figures 3 and 4 represent the growths obtained in these experiments. The number of tests made indicates clearly that crown gall tissue formation may be induced in this manner. The galls formed, how-

ever, are due entirely to the proliferation of the host rather than the inoculum. The percentage of galls formed from second and third generation crown galls is small. This may be accounted for by the lateness of the season, when the growth of the plant usually becomes retarded. This is consistent with the reports that crown gall formation depends in a large measure upon the capacity for growth of the inoculated tissue. Nine homeotransplant crown galls were produced from inocula of first generation crown galls in twenty-one inoculations, while only two crown galls were produced when the latter galls were used as inoculating material. Autotransplants of second generation crown galls produced six galls in as many inoculations and plants.

Ricinus crown galls produced by *B. tumefaciens* were further studied by transplanting pieces of this tissue to thirty-four young shoots of the tobacco plants, *N. Tabacum*. Crown galls^o were produced on five plants. One of these crown galls produced typical tobacco leaves. There was no evidence of the growth of the inocula.

TOMATO CROWN GALL

The behavior of tomato crown gall transplants was also studied in a similar manner. Crown galls on the tomato plant produced by *B. tumefaciens* of different cultural ages were used. In one case eleven homeotransplants were made, in the other case twenty-one homeotransplants were made. In all cases crown galls were observed on the hosts in thirty days. Figure 7 represents the stem of a pot-grown tomato plant inoculated with a small piece (2-3 mm.) of crown gall tissue produced by inoculation with *B. tumefaciens*. A longitudinal section through this stem seems to bear evidence for the limited growth of the inoculum. The margins of the stem of the host where the incision was made show excessive proliferation, indicating crown gall formation. In figure 8, a more vigorous garden-grown tomato stem is shown that had been inoculated with tomato crown gall tissue. The inoculum was introduced into a perforation made in the stem. Two masses of crown gall tissue appear on both sides of the stem. Figure 9 represents a similarly treated tomato stem. Here the inoculum may be seen held between the two masses of crown gall tissue, but is not a part of the new

crown gall. A longitudinal view of a similarly inoculated stem shown in figures 8 and 9 is represented in figure 10. The necrotized inoculum may be seen in the pith in the lower section of the stem.

In these experiments a number of the transplants appear to be completely surrounded by the crown gall tissue formed by the host so that I found it difficult to determine whether or not the inoculum succeeded in establishing itself in the host. In the majority of cases a series of longitudinal sections through such stems showed the inoculum as a completely necrotized tissue in the center of the host-formed gall. In several cases, slight growth of the inoculum occurred. Microscopic examination of these galls showed, however, that the major portion of the crown gall was due to the overgrowth of the host.

Heterotransplants were made in which crown gall tissue of the tomato was introduced into growing portions of twenty-one tobacco plants (*N. Tabacum*). While a large number of these inoculated plants failed to show any reaction other than a callosus, seven plants produced well developed crown galls, three of which differentiated and formed typical leafy shoots of the tobacco. Figure 13a is a photograph of a tobacco stem with an inoculum of the tomato still visible. The wound has healed and the inoculum is dead. No crown gall is expected. In figure 13b two small crown galls are seen. These have been produced by a similar inoculum from the same tomato crown gall. The inoculum was introduced into the tobacco stem forty days earlier. In figures 14 and 16 well developed leafy crown galls may be seen. These arose after an inoculation with an inoculum from a tomato crown gall. In figure 16 a portion of the stem was removed to show the crown gall and its leaves more clearly. Figures 15a and 15b show entire and longitudinal section views of a tobacco stem similarly treated as above. The host tissue alone takes part in the formation of the crown gall. The inoculum is imbedded in the pith of the stem and is apparently dead.

Similar heterotransplants were made with the crown gall of the geranium and the tomato plant as the host. Figures 11 and 12 represent two views of a tomato plant inoculated with crown gall tissue of the geranium. Here also it is seen that while the host forms the crown gall the inoculum dies and

plays no further part in the development of the crown gall. The arrow in figure 11 indicates the position of the dead inoculum. The crown gall appears below it in the form of a small globular mass of tissue which on microscopic examination shows small parenchymatous cells.

Homeotransplants of geranium give similar results to those already described for the beet, *Ricinus*, and tomato. Plants such as the dahlia and potato, which failed to produce crown galls on inoculation with *B. tumefaciens*, failed to respond to inoculations with crown tissues of the geranium or tomato. A large number of inoculations were made.

In the above listed experiments, similar portions of the gall used for inoculation purposes were plated and in all cases *B. tumefaciens* was recovered, as determined by inoculations into healthy plants.

SUMMARY AND CONCLUSIONS

1. Auto-, homeo-, and heterotransplants of crown gall tissue are capable of exciting crown gall formation in the host when the host is capable of responding to inoculations of *B. tumefaciens*.

2. Crown gall tissue of the common garden beet may be grafted on the yellow mangel.

3. The graft or inoculum successful in establishing itself on the host is capable of further limited growth, but then it also stimulates the host to crown gall formation.

4. Crown gall transplants differ from the transplants of animal tumors in that the crown gall transplant does not form the sole substance of the new overgrowth. The stroma of the animal tumor has no analogy in the crown gall tissue. The fibrovascular elements found in the crown gall result from the differentiation of the parenchymatous tissue that makes up the crown gall.

5. Crown gall of the host after the introduction of an inoculum of crown gall tissue is not due to the growth of the inoculum, but results from the changes which succeed the introduction of *B. tumefaciens* with the inoculum. Plated cultures of parts of the crown gall tissue from which inocula were taken always yielded in my experiments an abundance of *B. tumefaciens* as

determined by culture studies, stained smears, and subsequent inoculations.

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Description of plates 12, 13

Plate 12

Fig. 1. *Ricinus* petiole inoculation with a single inoculum of crown gall tissue from the petiole of another *Ricinus* plant.

Fig. 2. Control inoculation made with an inoculum of normal tissue.

Figs. 3, 4. *Ricinus* petiole with crown gall of the second and third generations induced by crown gall inocula from the *Ricinus*.

Fig. 5. Crown gall on the *Ricinus* stem produced by inoculating a small piece of crown gall from sugar beet.

Fig. 6. A longitudinal section of the same stem. The necrotic area below the gall, indicated by the arrow, shows the region of the transplant.

Fig. 7. Tomato stem (grown in pot) inoculated with portion of crown gall developed on the same plant.

Fig. 8. Tomato stem (grown in field) inoculated with portion of crown gall from another tomato plant. Crown galls appear on both sides of the stem.

Fig. 9. A similar experiment in which the inoculum is still visible as a necrotized body between the two globular masses of crown gall tissue.

Fig. 10. A longitudinal section of a tomato stem showing necrotized pith of the host with small overgrowth arising from the cortex and epidermis.

Figs. 11, 12. Two views of a tomato stem (grown in pot) inoculated with crown gall of the geranium showing crown gall formation of the host.

Fig. 13 a. Tobacco stem with tomato crown gall inoculum. 13 b. Tobacco plant showing formation of small crown galls after inoculation with tomato crown gall.

Fig. 14. Tobacco stem showing the development of a leafy crown gall after inoculation with tomato crown gall.



LEVINE: CROWN GALL TRANSPLANTS

Plate 13

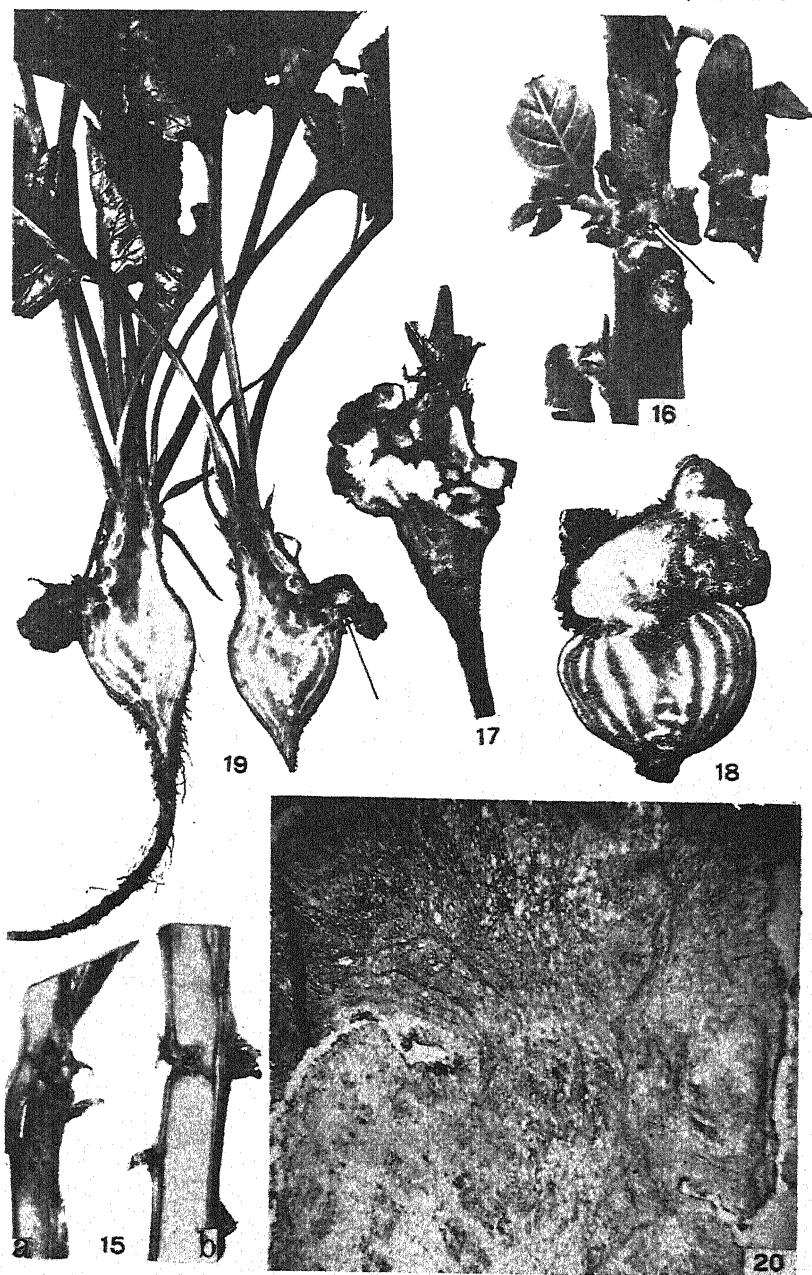
Fig. 15 *a*. Longitudinal section of tobacco plant inoculated with tomato crown gall, showing considerable callus tissue and a small crown gall. 15 *b*. A longitudinal section of a tobacco stem similarly treated showing the development of embryonic tobacco leaves arising from a small globular crown gall.

Fig. 16. A section of tobacco stem similar to one shown in figure 14. The stem was cut so as to expose the globular crown gall from which a leafy shoot has arisen. The stem was inoculated with a piece of tomato crown gall tissue. The removed portion of the stem is shown to the right in the figure.

Figs. 17, 18. Colossal long red mangel and a garden beet respectively, with crown gall, resulting from an inoculation with a virulent strain of *B. tumefaciens*. Both figures indicate the absence of pigment in the center of the crown galls, or show only a small diffused quantity of pigment as compared with the surface of the gall and normal root.

Fig. 19. Yellow tankard mangel, showing growth of a transplanted garden beet crown gall tissue. The arrow indicates the presence of yellow pigmented tissue of the yellow mangel.

Fig. 20. Microscopical section of the root of the yellow mangel in the region of the union of the host and crown gall tissue of the garden beet, showing an excessive proliferation of the host and the transplant (photograph made with the aid of obj. 32mm., oc. K 20, bellows 55 cm., filter K 2, W.W. panchromatic plate).



LEVINE; CROWN GALL TRANSPLANTS

Notes on *Arundinaria*

CLAIR A. BROWN

The manuals on the flora of the eastern and southern United States include two species of 'cane' or native bamboo, namely, *Arundinaria macrosperma* Michx. and *Arundinaria tecta* (Walt.) Muhl., both of which are supposed to flower at irregular intervals.

Characteristics usually used for separating these two species are as follows: *A. tecta* has canes less than ten feet tall with flowers developing in terminal panicles on radical shoots, while *A. macrosperma* has canes more than ten feet tall, with flowers developing in lateral panicles on the old canes.

From time to time questions have been raised in regard to the identity of these species. In their discussion of them, Scribner and Merrill¹ state that:

A. tecta has been treated by some authors as a variety of *A. gigantea* (*A. macrosperma*). Although possibly not specifically distinct, the two are found growing together under like conditions, and under these circumstances the one is readily distinguished from the other. Rarely found in bloom.

Recently, Harper² has made the following statement:

This genus (*Arundinaria*) is not fully understood, partly on account of the scarcity of flowers and seed, and the number of species in North America may be anywhere from one to three or four. In Alabama there seems to be two possibly three.

He gave a description of these forms including three illustrations.

In regard to the irregular flowering of one of the species of *Arundinaria* Cocks³ wrote as follows:

In view of the fact that it is so often stated that this plant [*A. tecta*] blooms only at intervals of several or many years, it is worth noticing that certain clumps have been observed by the writer near Abita Springs, which have bloomed every year in the latter part of May, since 1899.

¹ SCRIBNER AND MERRILL. Grasses of Tennessee p. 128. 1894.

² HARPER, R. M. Monograph of the economic botany of Alabama p. 72-77. 1928.

³ Cocks, R. S. Annotated catalogue of grasses growing without cultivation in Louisiana. Gulf Biologic Station Bull. 10: 40. 1908.

On account of the difficulty of determining with any degree of satisfaction specimens of *Arundinaria* collected in South Louisiana, a study has been made of the genus. Spikelets of *Arundinaria* were first collected by the writer in March, 1927, in a canebrake near Baton Rouge, Louisiana (no. 989). These were from the lower nodes of old canes that had been cut off one or two joints above the ground.

In November, 1927, a considerable portion of the canebrake in which the above specimens were collected was cleared. During the last of March and April, 1928, flowers were again found on the lower nodes of the cane stubble. For the purpose of comparison a specimen of *A. macrosperma* was then obtained from Professor A. S. Hitchcock. In the letter accompanying the specimen, Professor Hitchcock wrote: 'I have not been able to separate *A. macrosperma* and *A. tecta* in an entirely satisfactory manner. . . . I am sending you a specimen I take to be *A. macrosperma*.' When the specimen was examined it appeared to be identical with the Louisiana specimens which had been recently collected and which had been called *A. tecta*.

About the first of May there appeared in the same field a large number of somewhat shrubby radical shoots which bore terminal panicles, and according to the manuals should be *A. tecta*. An examination was then made of the canebrakes near Baton Rouge, Louisiana, and in several places flowering specimens typical of *A. macrosperma* were found. As it appeared that flowers of the two species had been collected, material of each was sent to the Grass Herbarium in Washington. The radical shoot form (no. 2112) was identified as *A. tecta*,⁴ and the form with flowers on the old canes (no. 2125) as *A. macrosperma*.

In one of the places where the cane was found in bloom a drainage ditch had been dug in the early part of January, 1928. In this place, flowers were found both on radical shoots and on the old canes. On digging up some of the plants, it was found that some radical shoots with flowers (*A. tecta*) came from the same rootstock as did stalks with lateral spikelets (*A. macrosperma*).

⁴ Identical with figure 1, in The Genera of Grasses of the United States, by A. S. Hitchcock.

With the idea that flowers of *Arundinaria* could be produced by cutting off the old canes at certain seasons, or by reducing the water supply as was done by the drainage ditch, several canes were cut in November, 1928, in the place where *A. macrosperma* (no. 2125) was collected. In the spring of 1929, the place was visited again and it was found that the canes which had been cut off from one to three joints above the ground had flowered from the lower nodes.

A careful examination of several other canebrakes in flower during the spring of 1929 has resulted in finding flowering radical shoots attached to the same rootstock as the old flowering canes. One collection (no. 2435) was made near Erwinville, Louisiana, on the edge of a thicket which had not been cut or drained for several years. This suggested that both forms of *Arundinaria* may occur on the same rootstock naturally and that cutting or some other stimulation may not be necessary.

Another point mentioned in the literature is that the old canes of *A. macrosperma* die after they fruit. This differs from the recent observations. Canes that were known to flower in 1928 were cut in the fall and next to them were left some that were not cut. Both remained alive, and in April, 1929 the stubble of the cut canes flowered from the lower nodes, as has been stated.

One might inquire as to the reason for the difference in size between the small woody canes the size of a lead pencil and only a few feet tall and the large woody canes one to one and a half inches in diameter and up to thirty feet tall. It has been noticed that there are many patches of this small type. The only explanation that can be offered is that there must be some difference in soil or moisture conditions which hinders the growth of these plants.

Since it seems certain that the different forms of *Arundinaria* which in the past have been considered two distinct species are in reality but one, it becomes necessary to decide which name is valid. Professor A. S. Hitchcock has kindly written the following opinion concerning the valid name: 'In 1788 Walter published two species of *Arundo*, the first *Arundo gigantea*, the second *Arundo tecta*. *Arundo tecta* was transferred to *Arundinaria* by Muhlenberg in 1817. *Arundinaria gigantea* was described by Chapman in 1860, but there is no evidence that this was based upon

Arundo gigantea of Walter. Under the rules of nomenclature it would be necessary to consider this as an independent description, consequently *Arundo gigantea* Walter cannot be transferred to *Arundinaria* because of the presence of *Arundinaria gigantea* Chapm. Although the names are the same and the species probably identical they must be looked upon as independent names. Consequently *Arundinaria gigantea* cannot be taken up. The valid name for the large cane then becomes *Arundinaria macrosperma* Michx., 1803. Since *Arundo tecta* is the older name, dating from 1788, it would seem necessary to take up this if the two forms are considered as one species.'

It would seem then, that the name *Arundinaria tecta* (Walt.) Muhl. should be used for the common southern cane or bamboo, and that the description should be changed so as to include the characters which have been previously used for both *A. tecta* and *A. macrosperma*.

The writer wishes to acknowledge his indebtedness to Professor A. S. Hitchcock for his identifications and opinion on the valid name; and to Dr. C. W. Edgerton for his helpful criticisms.

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Development of the pollen grain and the embryo sac of *Agropyron repens*

MAY MOWERY

(WITH PLATES 14, 15)

Agropyron repens L., known under several different popular names, but commonly as quack grass, is a close relative of wheat. Its history as an Old World pest as far back as there is definite record, its characteristics and habits, methods of control, etc. have been treated by Kephart (1923), who regards it as the most notorious of all weeds, with the possible exception of the Canada thistle.

Material for this morphological study was collected and fixed during the summers of 1925 and 1926. Two methods of dissection were used: first, removing the lemma, and fixing the palea, with the enclosed flower, second, removing both lemma and palea and fixing only the essential organs. The first method proved most satisfactory, especially for younger stages. For fixation, Flemming's weaker solution and Allen's modification of Bouin's both gave good results. The material was imbedded in paraffin, cut at eight to twelve microns, and stained in iron haematoxylin.

MICROSPOROGENESIS

The microsporangium is derived from the outer layer of the periblem, as is usual in angiosperms. There are three stamens in each floret. The development of the anther is typical, and like that of the wheat as described by Percival (1921) in *The Wheat Plant*. The anthers develop in spring, growing rapidly just before anthesis, as becomes evident from the stages found in a young spike in June: longitudinal sections of a spikelet similar to that outlined in Percival's figure 92 (page 115) then show three florets in which sporogenous tissue has differentiated, and two primordial flowers: the fifth floret does not develop. In the climate of southern Minnesota anthesis occurs from the middle to the last of June. At first a homogenous mass of meristematic cells covered by an epidermis becomes four-lobed at an early stage. The sporogenous tissue developing from the outer layer of the periblem appears at the time the lobes become evident. The divisions previous to the formation of the spore-mother-cell

occur rapidly. The radially elongated cells divide equally and almost simultaneously, by periclinal walls, forming a primary parietal layer which forms the wall of the anther, and a primary sporogenous layer. The primary parietal layer divides to form the endothecium, a middle layer, and the tapetum. The formation of the tapetum, coincident with the spore-mother-cell stage, reaches its maximum at the tetrad stage of the spore-mother-cell, at which time it is a prominent layer of two-nucleate cells. After the sporogenous tissue has divided to form the spore-mother-cells, they grow larger and round up somewhat. Then follows the heterotypic division.

The nuclei of both the vegetative cells and the cells of the sporogenous tissue are characterized in *Agropyron repens* by several distinct nucleoli. The nucleus of the microspore-mother-cell shows a network upon which are distributed chromatin granules, and one distinct globular nucleolus. The chromatin granules take a definite stain. The cytoplasm of the spore-mother-cells does not appear to be as dense as that of the tapetal cells, which are easily distinguishable by their heavier stain. It appears to be a fine network with small granules, which does not take the stain readily. In figure 1, the nuclear net is quite pronounced, its strands having become noticeably thick. Figure 2 represents a stage of synizesis in which the nucleolus, although centrally located, is discernible. In figure 3 the granules are distinctly massed and appear to be made of larger lumps, with a large nucleolus lying just outside the mass, which shows clearly the forming spireme. In figure 4 there is evidence of a longitudinal split in the thickened spireme, as well as indications of breaking up into chromosomes. As the thread breaks up into rod-like chromosomes the nuclear membrane disappears, but the nucleolus still persists. The spindle appears as a number of fibers which attach themselves to the chromosomes and converge at the poles. Figure 5 shows late anaphase, the rod-like chromosomes being very prominent as they approach the poles.

During the heterotypic division, usually only one stage is represented in an anther at any one time. In the homotypic division, this is not the case; for two or three stages of mitosis are represented in one longitudinal section. The chromosomes at the time of anaphase (figs. 7, 8) appear as slender bodies often somewhat U-shaped, two of them remaining away from the gen-

eral mass. The count made from this stage, using Belling's method, was twenty-one. The formation of the cell walls is successive (figs. 6-9). The four granddaughter nuclei (fig. 9) are alike in size, amount of chromatin, and in having several nucleoli. These grow to twice their first diameter (fig. 10) but in other respects appear much the same. The cytoplasm in these cells as well as in the tetrads has a distinctly radial tendency.

After the two divisions the young microspores become invested by a wall independent of the wall of the mother cell. This soon becomes differentiated into two layers, the intine of cellulose and the outer cutinized exine.

The first new feature in the development of the microgametophyte is the appearance of the germinal aperture, a thin spot in the exine, which can be discerned before the nucleus enlarges prior to division. This single aperture is characteristic of pollen of Gramineae (figured by Percival, 1921, for *Triticum*). When the nucleus divides, it forms the tube nucleus which is characterized by a single nucleolus, and the generative nucleus, which divides immediately to form the sperm nuclei, which at first appear small (fig. 11), but inclosing large nucleoli. The wall now becomes thicker and somewhat sculptured, and the sperm nuclei lengthen out. Figure 12 shows the appearance of the male gametophyte at the time the pollen is shed.

MEGASPOROGENESIS

The megasporangium originates as does the microsporangium on the outermost layer of the periblem. At first the epidermis of the member upon which the ovule is to appear is even. Cell division in the epidermis at first radial but in different directions in the hypodermal layer causes a slight protuberance. This becomes more and more evident and constitutes the nucellus of the forming ovule (fig. 13). Soon one of the hypodermal cells becomes slightly enlarged and takes a deeper stain, indicating its sporogenous nature (fig. 14). This cell enlarges so that by the time it begins to divide it is about four times the size it was when it first began to differentiate from the other cells. About this time a slight protuberance at the base of the nucellus indicates the first integument. The beginning of the second integument shows soon after the appearance of the first.

It is generally stated that ovules of Gramineae have no funiculus, but it would be impossible to draw an exact line between its presence and absence. The writer found very slight indication of a funiculus in *Agropyron repens*, merely a few slightly elongated cells at the broad region of attachment. This placental region appears to be not quite so broad here as in the case of wheat and some other grasses. The ovule attains a form which might be described as half-anatropous (fig. 20), except that the raphe characteristically present in such a type appears to be undeveloped here.¹

The archesporium, which first became evident by its larger size and deeper stain, is in this case a single cell. There is no record of an archesporium of more than one cell among monocotyledons, with one or two exceptions reported by Coulter and Chamberlain (1903). *Agropyron repens* is typical in this respect. The development of the archesporium differs from that of the microsporangium in that there is no parietal tissue developed, nor does the primary sporogenous cell divide to form a number of sporogenous cells, so that the archesporial cell is the spore-mother-cell. In *Agropyron repens* this archesporial cell increases in size so that it becomes very prominent (fig. 15). This divides twice by periclinal walls, forming a row of four megaspores (fig. 16). The first division is the reduction division. Three of the megaspores nearest the micropyle degenerate and the one farthest away enlarges to become the embryo sac (fig. 17). One slide showed the megaspore nearest the micropyle in telophase, while the other three showed indications of mitosis. There was not enough evidence to show whether this was merely an abnormal cell or not. The nucleus in the embryo sac divides three times in rapid succession, forming an eight-nucleate sac (figs. 18, 19, 20).

¹The ovule in *Avena*, *Triticum*, and *Zea* is characterized by True (1893) as campylotropous, and similarly that of *Poa* is designated simply as campylotropous by Miss Andersen (1927); while Hackel (in Engler and Prantl) and Rendle (in his *Classification of Flowering Plants*) describe the ovule for grasses in general as slightly campylotropous. On the other hand, Percival calls the ovule of *Triticum* anatropous, and VanTieghem also speaks of it as anatropous or half-anatropous for the family. The published illustrations are somewhat at variance with either of these types, and indicate that the grass ovule is of a rather anomalous character, which should not be forced into any of the conventional categories.

When eight nuclei have been formed, one from each end moves toward the center of the sac and walls are laid down around the nuclei remaining at each end. The two polar nuclei do not fuse before fertilization, but they remain close together and approach the egg cell at that time. The three antipodal cells divide to form antipodal tissue, ranging from ten to sixteen cells (fig. 21). These cells are large, with distinct cell walls surrounding a darkly stained mass of cytoplasm. The nuclei take a lighter stain and contain from one to three distinct nucleoli. This is in line with the three strongly developed antipodal cells reported by Miss Andersen (1927) in *Poa pratensis* and *Poa compressa*, and the report of Weatherwax (1926) of antipodal tissue in maize, and of Cannon (1900) in *Avena*. The embryo sac at this time has enlarged, but the nucellus still remains and a definite nutritive jacket of deeply staining cells surrounds the embryo sac, which is egg-shaped with the micropylar end smaller. The larger end is filled with antipodal tissue. The question of fertilization is one of the problems which should be investigated at a later date, together with the fate of the antipodal tissue.

The fruit of *Agropyron* is a typical caryopsis, or one-celled dry indehiscent fruit with a thin membranous pericarp adhering closely to the seed, so that fruit and seed are incorporated in one body forming a single grain (True, 1893). A few experiments were tried to determine how soon after maturity seeds would germinate. Tests were made in September, as soon as the spikes were collected, in October, and in November, with no results. In January, 1927, however, fruits collected in the summers of 1925 and 1926 were found to germinate. These fruits were dissected from the spikes and put in a moist dark place, where an even temperature was maintained. Of thirty-three fruits from a spike of twenty-two spikelets collected in 1926 all but one germinated. Of seventeen fruits from a spike of eighteen spikelets collected in 1925 all but three germinated. In the spikelets dissected usually only one or two mature fruits were found, rarely three or none. In the the spikes dissected there were fruits differing from the typical light brown ones in being more slender, with greater variation as to length, and in being black. Fourteen of the black fruits ranged in length from 1.5 mm. to 5 mm. while sixty-one light brown fruits ranged from 2.5 mm. to 4 mm. None of the black

fruits germinated, so they may have contained some dominant lethal factor or some fungus growth.

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Explanation of plates 14, 15

PLATE 14. Microsporogenesis (figures $\times 1080$ approximately).

Figs. 1-4. Formation of spireme thread, and division into chromosomes.

Fig. 5. Spindle: metaphase, first division.

Fig. 6. Telophase, first division, formation of cell plate.

Figs. 7, 8. Spindle, showing grouping of chromosomes, second division.

Fig. 9. Tetrad of microspores.

Fig. 10. Separate microspore.

Figs. 11, 12. Male gametophyte.

PLATE 15. Megasporogenesis (figs. 13-19, $\times 730$; figs. 20, 21 $\times 73$).

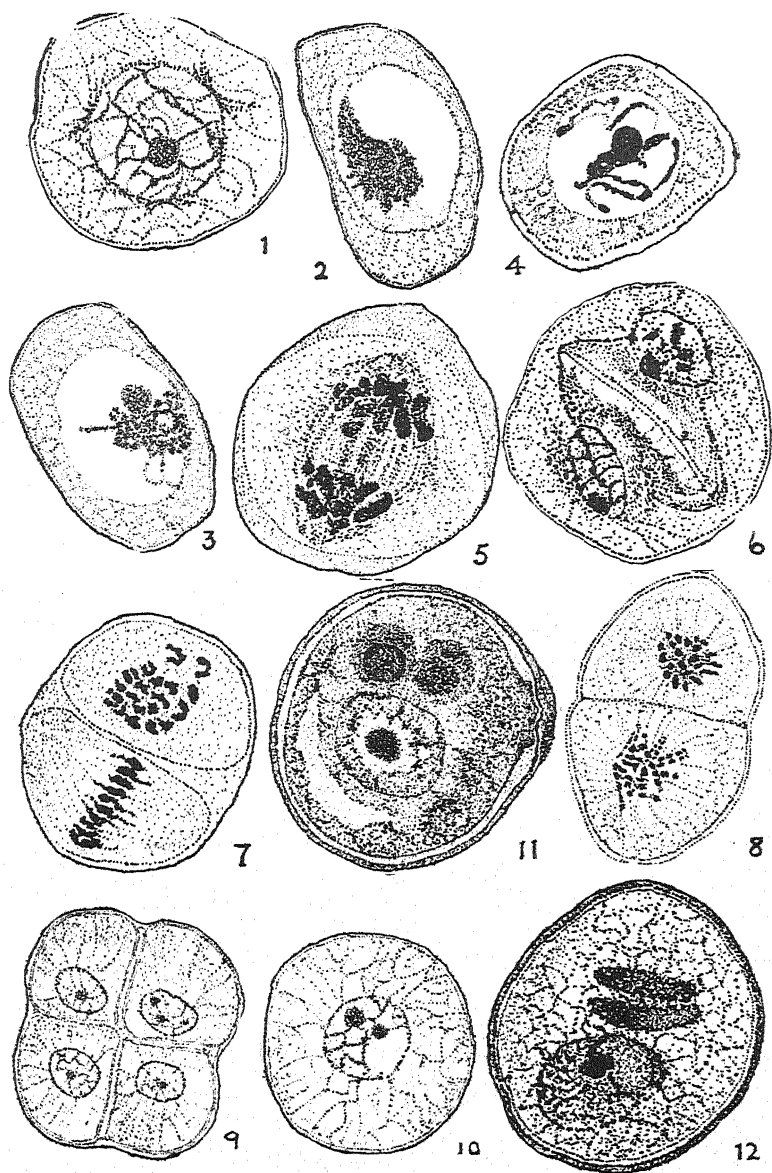
Fig. 13. Early stage in forming ovule.

Figs. 14, 15. Archesporeal cell.

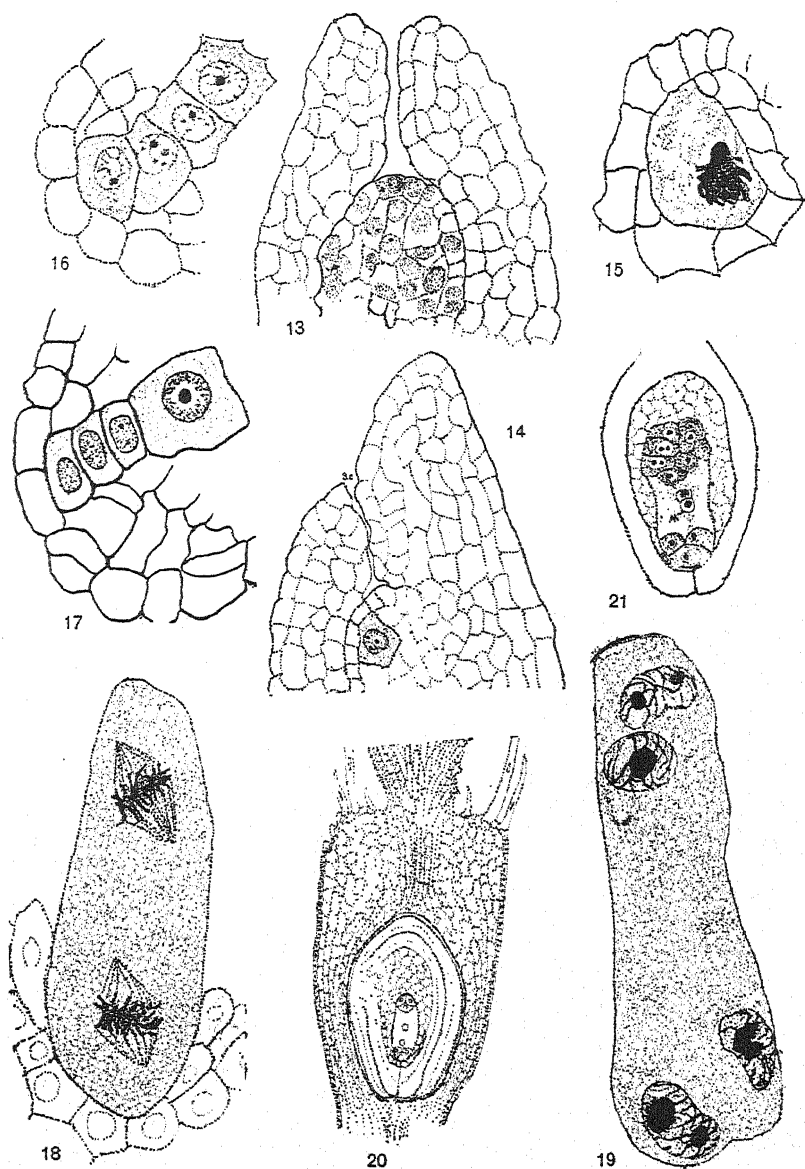
Figs. 16, 17. Megaspore tetrad and enlargement of functional spore.

Figs. 18-20. Embryo sac development.

Fig. 21. Female gametophyte, showing egg apparatus, antipodal tissue, and polar nuclei.



MOWERY: AGROPYRON REPENS



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The origin of symmetry patterns of pollen grains

R. P. WODEHOUSE

(WITH PLATE 16 AND FOUR TEXT FIGURES)

Of the many characters of pollen grains which make up their remarkably varied forms, some are encountered again and again in entirely unrelated groups, and without hint of genetic continuity; while others are strictly phylogenetic, occurring only in groups with ancestral affinity. All heavy-walled pollen grains have one or more germinal apertures—thin spots or holes in the exine through which the pollen tube may emerge. The number and arrangement of these is found to be the same in many unrelated groups; and, though these characters are generally constant throughout any group such as a tribe or family, frequently more than one number and arrangement of apertures is found within a family—or more closely related group—or even among the different individuals of a species. At the same time, however, certain less conspicuous characters, as the sculpturing, texture and various adornments of the exine, are generally restricted in their phylogenetic distribution and are always extremely constant for any species, and are of great value in determining phylogenetic relationships (Wodehouse, 1928).

Pollen grains are single cells, and such observations as these can best be interpreted in the light of our understanding of other plant cells. Any cell possesses two sets of characters. For example, if a fragment of wood be examined microscopically, its cells are seen to possess certain characters which distinguish them at once from those of all other tissues. On the other hand a more minute examination with the microscope will nearly always reveal one or more characters which are phylogenetic, and enable one to tell the family, genus, or possibly even the species to which the wood belongs. For example the pitting, various perforations, and secondary thickenings on the walls of certain wood cells exhibit a wide range of variation in size, shape, and arrangement, and possess high value for purposes of classification and identification of woods (Record, 1919).

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For our first clear understanding and concise statement of the origin of such classes of characters we are indebted to Harper (1918), who states that at least two sets of factors are involved in determining the form of cells, their internally determined or specifically inherited cell form—including their capacity to respond to stimuli—, and their contact and other relations with their neighbors during growth. This latter involves especially the conflict between the laws of cell bipartition with rectangular intersection of the successive planes of division on the one hand, and on the other the tendency of single cells and groups of cells to assume least surface configurations.

The problem as to which of the great variety of characters found among pollen grains are specifically inherited, and which are the result of interrelations with their neighbors can thus be quite sharply defined; and since there appear to be no words to designate adequately these two classes of cell characters I propose to call those which are the result of specifically inherited cell form *emphytic* (ἐμφυτος, innate), and those which are due to contact and other relations with their neighbors during growth, *haptotypic* (ἅπτειν, touch, and τυπώ, make an impression). Emphytic cell characters are usually strictly phylogenetic in distribution and consequently of high diagnostic value, while haptotypic cell characters are almost fortuitous in their distribution and of much less diagnostic value, but are of the greatest histogenetic interest.

The pollen grains of the great majority of dicotyledons are characterized by the possession of three symmetrically arranged longitudinal furrows (i.e. they are tricolpate), which serve either directly as germ pores, or each encloses a germ pore. Though these furrows vary greatly in length, they are generally long enough to permit them to serve as expansion folds; on the other hand they are occasionally so short that it is barely possible to distinguish which is the long axis. Nevertheless, whether they be long or short, broad or narrow, shallow or deep, they are always equally spaced on the equator of the grain, with their long axes crossing it at right angles and converging towards the poles. Some idea of the relative frequency of furrows in threes among pollen grains can perhaps be gained from the work of Hugo Fischer (1890). He has described the grains of 2214 species taken apparently more or

less at random throughout the entire group of flowering plants, and of these 1180 are tricolpate.

Though three is the characteristic number of germinal furrows, it is a significant fact that in the pollen of many plants are also found a varying number of grains with four, six, or two. Most frequently those with aberrant numbers of furrows make up only a small proportion of the grains and attract attention merely as curiosities; but in some species as, for example, the sorrel dock and white ash, almost—if not quite—one half of the grains have four germinal furrows. In the four species of *Dahlia* which I have examined, the number of furrows is always six, despite the fact that three is almost the universal number throughout the Compositae; and in one specimen of *Stenotus lanuginosus* which I have examined, approximately one half of the grains have two germinal furrows.

Why should three be the characteristic number of apertures among dicotyledonous pollen grains; and how do the other numbers originate? In the formation of pollen grains the pollen mother cell nucleus always goes through two successive divisions and nearly always gives rise to four daughter cells, producing in due course four mature pollen grains. Of course there are well known exceptions: in *Carex*, for example, three of the nuclei degenerate and the pollen mother cell becomes, as it were, transformed directly into the pollen grain; occasionally one or more of the daughter nuclei may divide once or twice, giving rise to five or more grains; or, as in the case of the Acacias, all four of the daughter cells divide once or twice more, giving rise to eight or sixteen pollen cells. Nevertheless the prevailing number of pollen grains produced by a pollen mother cell is four.

In the dicotyledons these four cells are formed after two nuclear divisions which take place in rapid succession, at right angles to each other, without the formation of dividing cell walls until after the four daughter nuclei have separated and reorganized. Regardless of the relative orientation of the spindles, the daughter nuclei generally tend to take up positions as far from each other as possible within the confines of the pollen mother-cell wall, which results in the tetrahedral arrangement. Other arrangements sometimes occur; in fact all pos-

sible arrangements of four cells in contact are found, but in the vast majority of dicotyledons the arrangement is prevailingly tetrahedral, and it is in this position that the phragmoplasts are formed and the cells rounded off and separated.

If four spheres are placed together in the tetrahedral position it will be seen that each must make contact with its three neighbors, giving each sphere three equally spaced contact points (text fig. 7). This suggests an explanation of the prevailingly tricolpate character of the dicotyledonous pollen grains. Furthermore such a suggestion seems plausible by comparison with the formation of germinal pores in some Basidiomycetes. For example, Dodge (1924) describes the formation of pore plugs in spores of *Gymnosporangium*, which he states are analogous to the caps which cover the germ pores

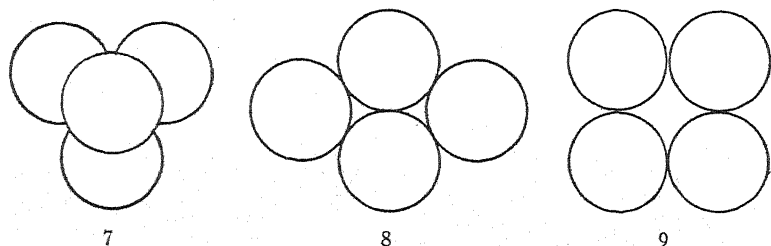


Fig. 7. Diagram of four spheres in contact in the tetrahedral arrangement. Each makes three points of contact, one with each of its neighbors.

Fig. 8. Diagram of four spheres in contact in the rhomboidal or half tetrahedral arrangement. Two make contact with two, and two make contact with three of their neighbors.

Fig. 9. Diagram of four spheres in contact in the tetragonal arrangement. Each makes contact with only two of its neighbors.

in pollen grains of *Cucurbita*. His figures show clearly that these pore plugs, and consequently the pores, are formed at the points of contact between adjacent cells.

For purposes of discussing the symmetry relations of these spheres it is convenient to speak of their polar axes as lines extending through the centers of the spheres and directed towards the center of the tetrahedron where they would all four meet, if so extended. Thus each sphere comes to have an inner and an outer pole, a proximal and distal polar hemisphere, and the equator is the line encircling the sphere midway between the poles—the boundary between the two polar hemi-

spheres. In the case of the four spheres, the three points of contact on each form an equilateral triangle, all in one polar hemisphere; whereas the three furrows in dicotyledonous pollen grains are on the equator—midway between the poles.

Now let us see what the situation is in pollen in which the four cells of the tetrad do not separate at maturity. Such a case is found in the pollen grains of nearly all the Ericaceae; for example in the pollen of *Azalea* the four cells of the tetrad remain firmly united in the tetrahedral position, forming a four-celled compound pollen grain at maturity (plate 16, fig. 1). Each of the cells is much flattened against its neighbors of the tetrad so that—instead of making contact by points, as spheres do in this arrangement—these contacts are broad flat surfaces as if formed under so much pressure that the flattening extends very near or even quite to the equators of the grains. Each of the four cells has three germinal furrows contiguous and continuous with those of its three neighbors directly across the edges of their contact faces. Each furrow encloses a single germinal aperture at its point of contact with the furrow of the neighboring grain. If these four grains were to be separated from each other, and, with the relief of pressure, the flattened sides of their proximal hemispheres should round out, they would be in essential respects just like any other tricolpate dicotyledonous pollen grains. Obviously in this case the position of the furrows and apertures is determined by the tetrahedral arrangement of the grains in the tetrad group, and is therefore a haptotypic character.

Another example of four-celled pollen grains among the dicotyledons is that of *Salpiglossis sinuata* (fig. 2). The cells are in the tetrahedral position, but here the union is looser than in the grains of *Azalea*, as if formed under less pressure, and the contact faces are correspondingly less extended so that their edges do not nearly reach the equator. The furrows are spindle shaped, broadening out in the middle to contain the germinal aperture and tapering towards their proximal as well as their distal ends. Though they exactly meet each other on the line of contact between the flattened faces of the adjacent grains, their apertures are not at the edges of contact, as in the grains of *Azalea*, but are some distance from them on the equators of the individual grains. This shows that in these

grains the position of the furrows with relation to the equator of the grain is controlled by the contacts between adjacent grains, but the position of the furrows relative to the poles of the grain is independent of its contacts with its neighbors, i.e. they take a symmetrical position midway between the poles. Thus it is plain that in the grains of *Salpiglossis sinuata* mutual contacts exercise, so to speak, complete longitudinal control but no latitudinal control of the relative positions of the germinal apertures.

After the two divisions of the pollen mother-cell nucleus are complete, and the four nuclei, apparently through mutual repulsion, have taken up positions in the pollen mother cell as far apart as possible, and consequently in the tetrahedral position, Farr (1916) and others have noted that in some cases thickenings are formed on the inside of the pollen mother-cell wall

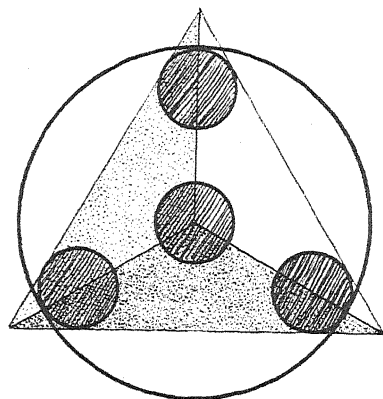


Fig. 10. Diagram of four daughter nuclei in the tetrahedral arrangement within the mother-cell wall, represented by the black circle. For explanation see text.

in the regions of least pressure. This can perhaps best be visualized if we think of the four nuclei contained within the spherical wall of the pollen mother cell as if situated at the four angles of an imaginary tetrahedron (text fig. 10). Such a figure is bounded by four plane surfaces—each an equilateral triangle—, six edges, and the four solid angles at which the four nuclei are situated. Now when the soft gelatinous inner layers of the mother-cell wall begin to swell, the viscous material is moulded inwardly into the form of the zones of least pressure which lie midway between each pair of nuclei. There are four such regions, each triangular and centering outside the centers of each of the triangular faces of such an imaginary tetrahedron. These four interior ridges of the mother-cell wall develop inwards and meet in the center of the tetrahedron. At this stage each of the four daughter

cells is still connected with its neighbors through three broad channels, six in all, each one lying in the center of the plane of compression between each pair of forming cells. As the thickening of the mother-cell wall proceeds the six broad connecting channels are progressively narrowed until, at the last stage before complete separation, the cells, which have now become rounded off, remain united by pit connections which lie in the same planes as the six edges of the assumed tetrahedron, and thus become the middle points of the contact faces of the new tetrahedral pollen cells. These pit connections are finally severed as the cells round up and become completely separated by the continued thickening of the pollen mother-cell wall. According to Farr (1916), Gates (1925) and others, this method of quadripartition by furrowing is common among the dicotyledons.

It is soon after the grains have separated that their sculpturing begins to appear. Its formation consists in the deposition, in organized form, of the material of the greatly thickened special mother-cell wall. As a general rule, in normal grains little or no suggestion of the pattern or hint of the position of the germinal apertures is discernible until after the separation and rounding up of the daughter cells is complete, and the material of the thickening of the special mother-cell wall has become packed between them; consequently from an examination of normal material, the relation of the germ pores to the points of mutual contact in grains which do not remain united is not generally apparent.

In pollen grains which exhibit a complicated system of sculpturing this nearly always presents a radiosymmetrical pattern which is definitely related to the germinal apertures. For example, in the normal grains of chicory there are three apertures and the pattern of the sculpturing is triradiate as in fig. 3; it is characterized by six prominent paraporal crests, so called because they are arranged, one on each side of the germinal pores. In aberrant grains in which there are more than three apertures the triradiate pattern is never found, which shows that the numerical type of the pattern is dependent upon the number of germinal apertures.

Fortunately in the development of the pollen grains of some varieties of chicory there are encountered many irregular

formations which show the nature of this relationship. These are of the kind which is generally regarded as denoting hybridity of origin. For example, in the variety known as 'Red-leaved Treviso,'¹ a large proportion of the pollen mother cells do not divide; in these the material of the special mother-cell walls is deposited in a granular concretion on the surface, but such cells appear to be deficient in power to properly organize it, and become formless giants without germinal apertures, and with no suggestion of the symmetrical pattern characteristic of the normal grains. Yet, at least in some cases, spines are weakly developed, and they and the texture of the exine bear an unmistakable resemblance to those of the normal grains. The symmetrical triradiate pattern is a haptotypic character and, lacking the contact stimuli, fails to develop, but the spines and texture are emphytic and develop, at least in part, independently of contact stimuli. These formless giants call to mind the giant spores and 'indurated asci' recently described by Dodge (1928) among the progeny of his hybrid *Neurosporas*. In these occasionally an ascus produces a single giant spore which bears the normal surface sculpturing, or the ascus fails to produce any spores, becoming instead indurated and with the surface markings laid down on the inside of the ascus wall.

In the anthers of the chicory flowers other pollen mother cells divide quite successfully, but the four daughter cells abort and become quite empty; nevertheless in these cases the pattern develops as typically as in the normal grains. A similar condition has been described by Tischler (1908) and others for the grains of sterile hybrids; if a pollen cell dies after only the first rudiments of the sculpturing are laid down, the pattern continues to form, and develops to completion even though the lumen of the pollen cell be quite empty.

Between these two extremes are a few other types in which irregular pollen mother cells appear to abort during the pro-

¹ I am indebted to Dr. A. B. Stout of the New York Botanical Garden, for the use of the slides upon which these observations of the developing chicory pollen grains were made. The plants were grown from seed obtained from Dippe Bros., Quedlinburg, Germany. It is interesting to note that they are characterized by excessive fasciation. See Stout, A.B., Duplication and cohesion in the main axis of *Cichorium Intybus*. Mem. Brooklyn Bot. Gard. 1: 480-485. 1918.

cess of separation of the four daughter cells. Occasionally this is found to take place when the furrowing has all but completed the separation of the cells; with the death of the protoplast they become frozen, so to speak, in the final act of separation when each of the daughter cells is still connected with each of its three neighbors by the pit connections which now become extended as six narrow tubes (fig. 4). Though the process of division is arrested with the death of the cell other processes continue on; the special mother-cell walls continue to thicken, and at their expense the pattern of the newly formed cells is carried nearly to completion, resulting in the phenomenon of four daughter cells still united in the tetrad, but with the pattern of the finished cells clearly defined. And in such cells the pattern exhibits triradial symmetry bearing the same relation to the three connecting tubes as in the normal grains it bears to the three germinal apertures.

Thus it appears that in the grains of chicory the type of symmetry is determined by the number and position of the germinal apertures and these in turn, are formed at the last points of communication between the adjoining cells. Since throughout the dicotyledons the tetrad formation is prevailingly tetrahedral, giving three points of contact, we have the explanation of the fact that the pattern on the pollen grains of dicotyledons is prevailingly triradial. This fact is the more remarkable since among floral and other symmetrical structures the pentagonal is the prevailing type of symmetry of the dicotyledons (see, for example, Blossfeldt, 1928), while the triradial or triangular, and hexagonal symmetries are quite rare. We are evidently dealing in this case with phenomena which are to be classed in fundamentally different categories.

As has already been pointed out in many species of dicotyledons, some pollen grains in a given anther may exhibit certain symmetries other than the triradial. Among the grains of species which are typically 3-colpate are frequently found a few grains that are 4-colpate, 6-colpate, and occasionally 2-colpate. How can these be related to tetrad formations?

It was well known to Nägeli (1842) that when pollen tetrads are formed, frequently there are a few in which the cells fail to get into the tetrahedral position. Two other arrangements which they may assume are the tetragonal and rhomboidal. In the tetragonal (text fig. 9) all cells are on the same plane,

and it is the arrangement that would result from bipartition with rectangular intersection with no indication of a tendency to readjustment toward a least surface configuration. In this grouping each cell makes only two points of contact with its neighbors. It is known to occur sometimes among dicotyledons and is normal for many monocotyledons. In the rhomboidal arrangement (text fig. 8) all four cells are in approximately the same plane but two cells make two points of contact and two make three points of contact. Such an arrangement would result from bipartition with rectangular intersection, as the tetragonal, but followed by a partially expressed tendency to assume the least surface configuration. This arrangement is called by Nägeli the half tetrahedral. These two types of divergence from the tetrahedral arrangement give either all four cells with two points of contact, or two cells with two and two with three points of contact. But so far in my experience, grains with two are the most rarely encountered of those with aberrant numbers of germinal furrows; only twice have I seen such cases (in the pollen of a single plant of *Stenotus languinosus*² and of *Hecastocleis Shockleyi*). The commonest aberrant number is four—a number of contacts which would seem to require at least five cells in a group. The production of supernumerary cells from the pollen mother cell appears to be a possible explanation, particularly if there are some 6-colpate grains found at the same time, but is less likely in the usual aberrants where only 3- and 4-colpate grains are found, since apparently the only number of cells which could consistently produce four contacts is five; if there should happen to be six grains formed in a group some would be 5-colpate, a number which is scarcely ever found.

An explanation of the origin of four germinal furrows is found in the developing chicory pollen; among the irregular grains are occasionally found some 'frozen' tetrads arrested in their development in the *tetragonal* arrangement with pit connections at only two points in each grain. In some few such cases the development of the external features of the grains has proceeded far enough to show quite definitely that two germinal pores were forming at the two points of contact, as would be expected, but there were also two more developing exactly opposite these points (pl. 16, fig. 5), so that each of

² A specimen collected in Oregon by Cusick (No. 3282).

these grains originating from the tetragonal arrangement would have four germinal apertures and consequently four furrows.

Thus we see that apertures are not confined exclusively in their development to the contact points of pit connections, but when these are in such a position that the cell would be asymmetrical, symmetry may be achieved by the development of supplementary apertures symmetrically placed.

The next commonest aberrant number of apertures is six; this is frequently found in grains of which the normal number is three. It is the characteristic number in the grains of *Dahlia*s which, in this respect, constitute a remarkable exception among the *Compositae*. The arrangement of these six apertures is always tetrahedral, (fig 6), in the sense that they occupy in these grains the same positions that the double furrows do in the tetrad grains of the *Ericaceae*—or that the pit connections do in the 'frozen' tetrahedral tetrads of the chicory. In other words the furrows lie with their long axes in the position of the six edges of the assumed tetrahedron. It will readily be seen that in this arrangement each aperture is subtended on the other side of the grain by another which is exactly opposite and with its long axis at right angles to the first. In chicory the cell apparently maintains its symmetry in the presence of two points of contact by developing four apertures. In the case of the *Dahlia* three points of contact apparently determine the development of three apertures, all in one hemisphere, and the cell maintains its symmetry by the development of three more exactly opposite these, resulting in the hexacolpate form of the *Dahlia* pollen grain.

These observations lead us to the conclusion that the number and arrangement of the germinal furrows in the grains of most dicotyledons is determined by the tetrahedral or other arrangement incident to their formation in tetrad. And, in as much as the numerical type of symmetry of the pattern is determined by the position and number of the germinal apertures, it may be stated that the number and arrangement of the elements in the symmetry patterns of pollen grains is a haptotypic character; that is to say is the result of their cellular interrelations and directly due to the conflict of the law of bipartition with rectangular intersection, contending with the tendency to assume the least surface configuration.

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Explanation of plate 16

All figures were drawn free-hand from studies made with a Zeiss 2 mm. apochromat objective, n.a. 1.3, and a 10X ocular.

Fig. 1. Pollen grain of *Asalea* showing four cells closely packed in the tetrahedral arrangement. Each of the three furrows of the individual cells is continuous with one furrow of each of its three neighbors and the apertures are formed at the edges of the contact faces.

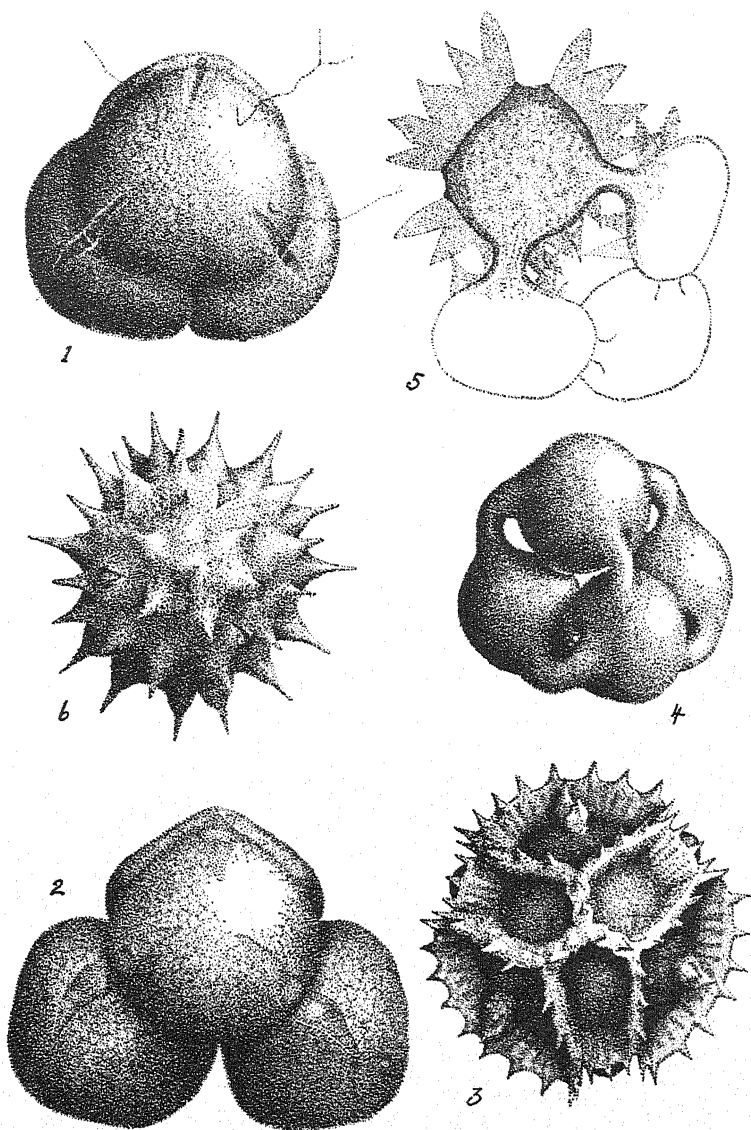
Fig. 2. Pollen grain of *Salpiglossis sinuata* showing four cells very loosely united in the tetrahedral arrangement. The furrows are continuous but the apertures are on the equators of the cells.

Fig. 3. Pollen grain of *Scolymus*, polar view, showing the three germinal apertures and triradiately symmetrical pattern. The pattern here shown is exactly duplicated on the other side, for proximal and distal hemispheres are always alike. This grain is essentially the same as that of chicory (cf. Wodehouse, 1928, pl. 20, fig. 14).

Fig. 4. A chicory pollen tetrad in the tetrahedral arrangement, arrested in its development by abortion, just before the final separation of the four daughter cells. The triradiate sculpturing has been omitted from the drawing.

Fig. 5. A chicory pollen tetrad in the tetragonal arrangement, optical section, showing the development of two accessory germ pores opposite the two pit connections.

Fig. 6. Pollen grain of tree *Dahlia*, showing three germinal furrows, all in one hemisphere, and with their axes directed radially in the figure. There are three more apertures in the other hemisphere, with their axes directed tangentially.



The flowering of Lemnaceae

ALBERT SAEGER

(WITH PLATES 17-19)

During the summers of 1927 and 1928 *Spirodela polyrhiza* (L.) Schleiden, *Lemna minor* L., and *Wolffia papulifera* C. H. Thompson were found abundantly in flower in a pond near Columbia, Missouri. While flowers of *L. minor* are not uncommon, those of *S. polyrhiza* have long been considered a botanical rarity, and flowering specimens of *W. papulifera* have, to the writer's knowledge, never before been reported.

Flowering in *S. polyrhiza* and *W. papulifera* is probably associated with some local conditions in the pond in which they are found. Although many other ponds within a radius of twenty miles were found with an abundance of *Spirodela*, and at least one other with *W. papulifera*, in none of them did a careful search reveal any flowering. The factors that are associated with the flowering of these Lemnaceae (duckweeds) are unknown, but sufficient observations have been made on this and other ponds to suggest experiments to determine their nature. These plants should serve as very favorable material for the study of flower production. They are small and can be grown under carefully controlled conditions, and they do not flower readily.

The family Lemnaceae includes four genera of about 26 known species. Records of their flowering follow.

SPIRODELA

Our knowledge concerning the flowers of *S. polyrhiza* is based largely upon a collection by W. H. Leggett (1870a).¹

¹ It is perhaps fitting, on the sixtieth anniversary of the discovery of flowers of *Spirodela* for the first time in America by Mr. Leggett, the founder of the Bulletin of the Torrey Club, to call attention to the fact that these notes on Lemnaceae brought out by Mr. Leggett and his correspondents were practically the first contributions to scientific botany published in this journal. The present editor has welcomed this historical review in the hope that it will stimulate a revival of interest in field observation and study of conditions of flowering in this family on the part of members of the Club and others. It may also be noted that this year marks the bicentenary of the publication of illustrations of flowers of *Lemna* by Micheli in Italy.—T. E. H.

He found them in July, 1869, in 'two little hollows filled with water' on Staten Island, New York, intermingled with *Lemna perpusilla* Torrey, also in bloom. Leggett sent specimens to John Torrey, G. Engelmann, C. F. Austin (who had written the account of the Lemnaceae in the newly published 5th edition of Gray's Manual), and to F. Hegelmaier, the monographer of the family. Dr. Torrey identified the plants and wrote: 'You have been very fortunate in detecting the flowers and fruit of a plant that is so rarely seen in such a condition, notwithstanding it is abundant in almost every part of the world.' Engelmann (1870) gave a somewhat detailed description of the flowers and fruit. Austin responded with a brief description of the fruit, accompanied by seven roughly drawn figures (Leggett, 1870b). Hegelmaier also identified the specimens as *S. polyrhiza* and commented:

The flowers and fruit of *Spirodela* rank among the greatest botanical rarities. I myself, though working some years on these plants, and examining rich materials of them both living and dried, have never before seen the flowers and fruit; and, in fact, they have been seen only by a few authors.

These authors were Willdenow (1805, p. 196), Schleiden (1839) in Germany, who found flowers with undeveloped pistils (pp. 386, 391); and Griffith (1851) in India, who described and illustrated the flowers and fruit of *Lemna major*, no doubt synonymous with *S. polyrhiza*. The discovery of the flowers of this species is credited by Wiggers (1780) to an enthusiastic young botanical student named Grauer, who had earlier found those of *Lemna gibba*. In the literature one also finds statements that Nees von Esenbeck had seen the flowers (Hoffmann, 1840, p. 230; Ludwig, 1909, p. 78).²

Some months after receiving a second lot of specimens (in alcohol) from Leggett, Hegelmaier (1871) published a detailed description of the flowers and fruit of *S. polyrhiza*.

² The statement that Linnaeus also had seen flowers of *Spirodela polyrhiza* is doubtless due to a misinterpretation of a note by Willdenow, loc. cit., in the so-called 4th edition of *Species Plantarum*: 'Flores Lemnae minoris et polyrhizae saepius vidi, Lemnae gibbae observarunt Ehrhart, Micheli et alii, hujus, nempe Lemnae trisulcae, primus omnium detexit Wolf, l.c. In *L. arrhiza* et obovata vero flores nemo adhuc vidit. W.' This signature of the initial 'W' shows clearly that the note is the personal statement of Willdenow. Wiggers (1780, p. 67), moreover, a late contemporary of Linnaeus, indicates that *Lemna minor* was the only species in which the latter saw flowers.

This is a comparative account of the floral structure of the species of *Lemnaceae*. In it he reconsiders his former view that the sexual complex is to be taken as an inflorescence, and now considers it a single flower. The plate accompanying his article gives a clear conception of the floral anatomy of *Spirodela*. The description and some of the figures are repeated in a later work (Hegelmaier, 1878). Brief reviews of Hegelmaier's account soon followed in Germany,³ and in the Bulletin of the Torrey Club by Engelmänn (1871*b*).

Spirodela was again seen in flower by Gillman (1871*b*). He found *Lemna minor*, *L. trisulca*, and *S. polyrhiza* (the last in the majority) blooming together in a pond on Belle Isle in the Detroit River, Michigan, July 30, 1871. Previously, June 7, 1870 he had found *L. minor* in flower at Eaton Rapids, Michigan. Ten years later on July 24, Gillman (1881) again found *S. polyrhiza* abundantly in flower in the same pond on Belle Isle. The flowers seen were in every stage of development up to the seed. He believed that the shade of overhanging vegetation favored the production of flowers, a view that does not agree with the writer's observations.

Rostowzew (1901), quoted by Ludwig (1909), must also have seen *S. polyrhiza* in flower in the vicinity of Moscow. Dalglish' (1926) states that the flowers of this species are unknown in Great Britain. Vuyck (1895*a*) found the species occurring commonly (Netherlands) but reproducing exclusively vegetatively.

Information concerning the flowering of the other species of *Spirodela* is also fragmentary. *S. punctata* (Meyer) Thompson was collected by Capt. Wilkes, U.S.N., at Tierra del Fuego, South America in 1839, and the flowers were described by Thompson (1898, p. 8). Kurz (1865) found *S. oligorhiza* Kurz in bloom, and gave a description accompanied by six figures, which Hegelmaier describes as 'äusserst roh.' The Australian species, *S. pusilla* Hegelm., is said to bloom more often than the others mentioned (Hegelmaier, 1895, p. 285).

LEMNA

The flowers and fruit of various species of *Lemna* have been studied more extensively. Micheli (1729), Ehrhart

³ H.S. Hegelmaier's Die Lemnaceen. Bot. Zeit. 27: 133-136. 1869.

(1779), Wolff (1801), Palisot (1816), Wilson (1830), Brongniart (1833), Richard (1833), Schleiden (1839), and Dalglish (1926) found the flowers of *L. gibba* L. The studies of Micheli, Wolff, Palisot, Richard, and Brongniart are accompanied by descriptive plates.⁴ Flowers of *L. minor* L. were known to Linnaeus (1763), Ehrhart (1779), and Schleiden (1839), and were described in detail by Wolff (1801), Ludwig (1881), Trelease (1882), Vuyck (1895a), Kalberlah (1895), and Rostowzew (1901, 1905). The latter's figures of the seed and embryo of *L. minor* are reproduced in Goebel's (1921) critical morphological study of Lemnaceae. Perhaps the most detailed study of the life history of any of the Lemnaceae is that of *L. minor* by Caldwell (1899). *L. trisulca* L. was seen in flower by Wolff (1801),⁵ Schleiden (1839, p. 386), Gillman (1871), Vuyck (1895), Kalberlah (1895), and Rostowzew (1901). *L. perpusilla* Torrey (1843), originally described from flowering plants collected on Staten Island, was again found blooming there by Leggett (1870a), as noted above; the development of its embryo has been studied by Blodgett (1914, 1923), who repeatedly found flowers, but did not publish the station. Hegelmaier (1895) reported having received plants of *L. valdiviana* Philippi with flowers and fruit collected in New Jersey by Austin.⁶ No doubt many others have observed species of this genus in flower.

Lemna minor, apparently, blooms quite readily. The writer has grown this species in all stages of flowering and fruiting through the months September to May in a dilute mineral solution such as that used for *Spirodela* in previous studies (Saeger, 1925). Concerning the causes of flowering in this instance one can only, in the absence of more experimental data, agree with Vuyck (1895a): 'Voorloopig wensch ik mij

⁴ Micheli's very clear figures (in his plate 11, fig. 1) of flowers of his plant described as *Lenticula palustris major, inferne magis convexa, fructu polyspermo*, found growing in abundance at Florence, are said by Ehrhart to agree very exactly with his flowering plants of *Lemna gibba* found at Hannover fifty years later. Linnaeus (1763, p. 1376) also accepts this plant of Micheli as identical with his *L. gibba*.

⁵ This Johann Friedrich Wolff (1778-1806), who knew the flowers of at least three species of *Lemna* is indicated by Pritzel and elsewhere as the man commemorated in the genus *Wolffia*, although not designated in the publication of the genus by Schleiden (1839).

⁶ This species was described as *L. Torreyi* Austin (seed included) in Gray's *Man. ed. 5. p. 479.1867.*

niet in onvruchtbare beschouwingen te verdiepen' (For the the present I do not wish to engage in fruitless speculation). Cultures of other species of *Lemna* grown under similar conditions have failed to flower.

WOLFFIA

The species of *Wolffia* known in the flowering state are: *W. brasiliensis* Weddell (1849); *W. arrhiza* (L.) Wimmer (Franchet, 1864); *W. columbiana* Karsten (1865); *W. hyalina* (Delile) Hegelm., *W. repanda* Hegelm., and *W. Welwitschii* Hegelmaier (1865, 1868). Weddell described in detail the flowers and fruit of *W. brasiliensis*, adding a plate of 27 figures. Karsten (1865, p. 103) based his description and figures of *W. columbiana* on flowering plants from South America: flowers were also reported from Detroit, Michigan by Austin (1870). The flowers of *W. microscopica* Griff. and of *W. cylindracea* Welw. are unknown.

W. papulifera Thompson is apparently known only from Missouri, having been collected by B. F. Bush near Kennett, in 1895, and in 1897 near Columbia, by C. H. Thompson (1898). The flowers were unknown until found by the writer during the summers of 1927 and 1928 (see plate 19). Sufficient material was collected at the time to serve as a basis for a study which it is hoped will be completed later.

WOLFFIELLA

In this genus of four known species no flowering has ever been observed. It would be of interest to know whether the sexual method of reproduction has been entirely replaced by the vegetative method, or whether fertile flowers might still be produced under appropriate conditions. Certainly there are some opportunities here for experimentation.

In the more recent instances where flowering of *Spirodela polyrrhiza* was observed (Leggett, Gillman, Saeger) it may be noted that there were always one or more other species of duckweeds blooming in the same pond, at about the same time (see plates 17, 18). Even the meager field observations made in each case indicate that some local conditions, characteristic of the particular pond in which the specimens occurred, were closely associated with the flowering of these plants. The indications are that the chemical composition of the pond

water is an important influencing factor. It is hoped that the production of flowers in *S. polyrhiza*, now a botanical rarity observed by a few, will become an experimental commonplace.

SUMMARY

1. The rarely observed occurrence of flowers of *Spirodela polyrhiza* (L.) Schleiden is again reported.

2. The occurrence of flowering specimens of *Wolffia papulifera* Thompson, hitherto unknown, is reported.

3. A brief review is given of flowering records of the species of Lemnaceae.

Thanks are here expressed to the Missouri Botanical Garden for the use of its extensive library and herbarium facilities.

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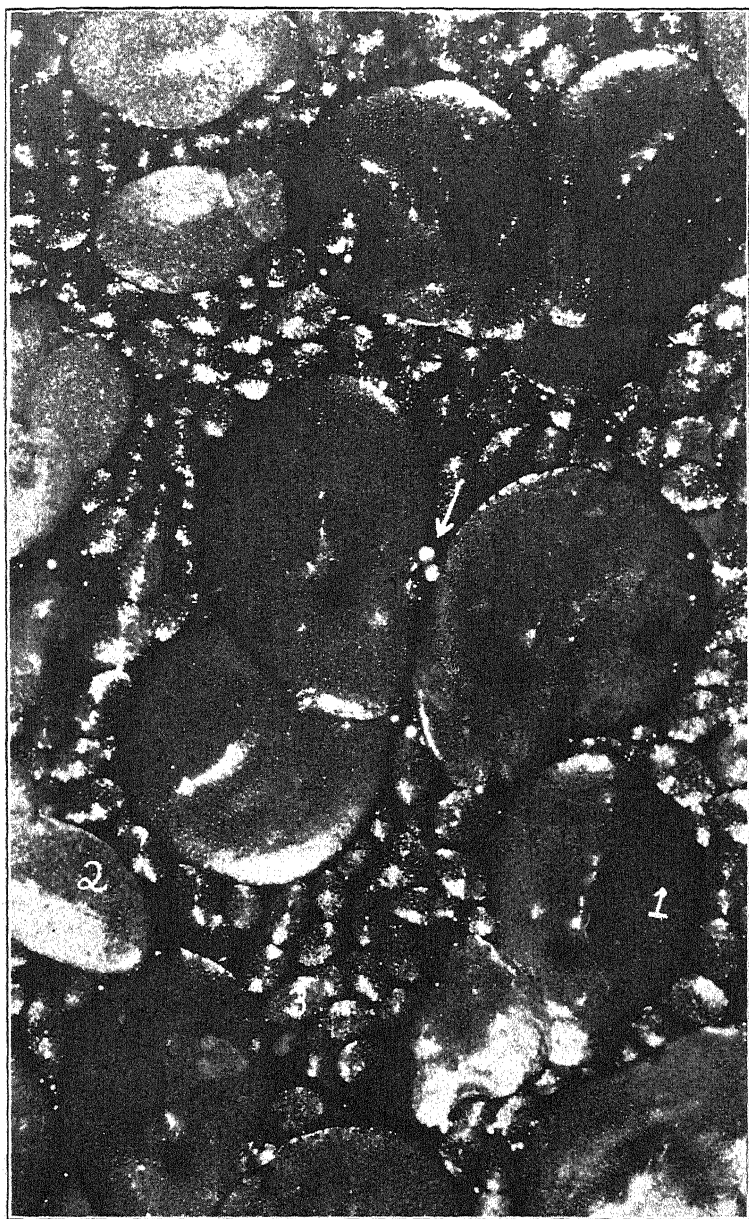
Explanation of plates 17-19

Plate 17. *Spirodela polyrhiza* (L.) Schleiden, a specimen in bloom: the arrow indicates the stamen, visible from above. Accompanying species: *Lemna minor* L. (2) and *Wolffia papulifera* Thompson (3).

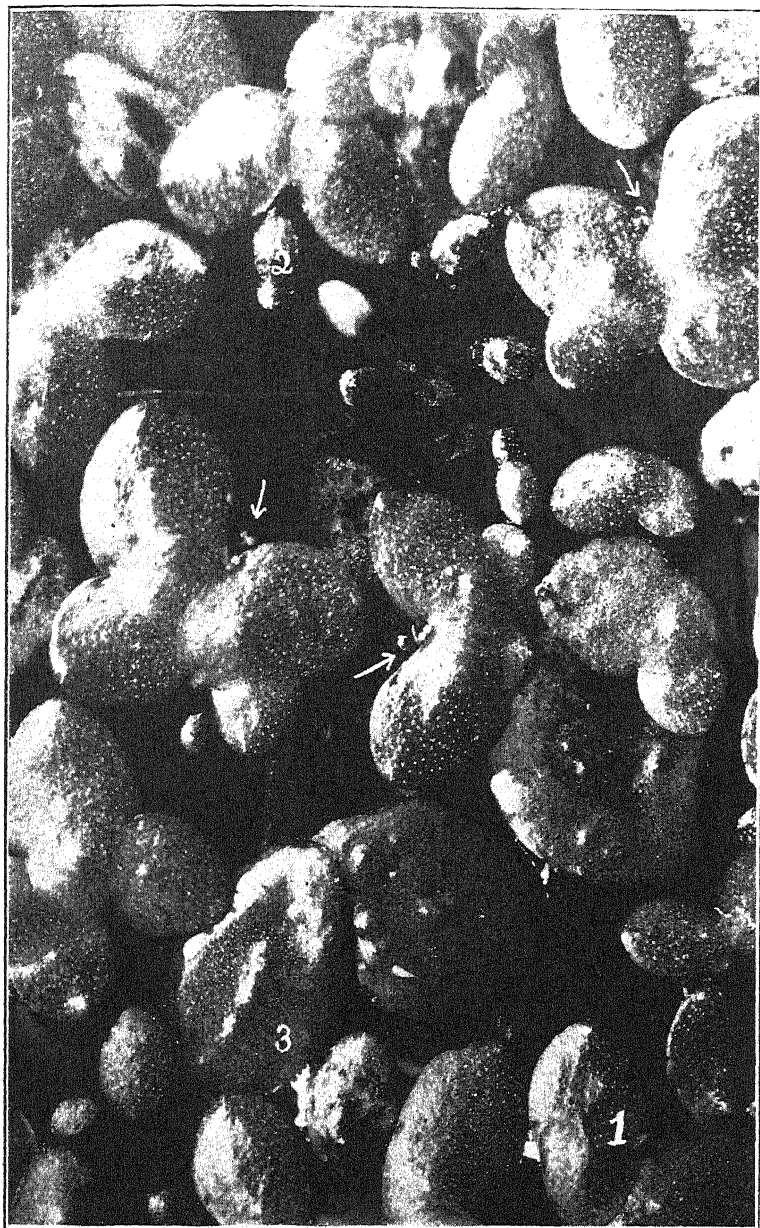
Plate 18. *Lemna minor* L., specimens in bloom: arrows indicate the stamens. Accompanying species: *Wolffia papulifera* Thompson (2) and *Spirodela polyrhiza* (L.) Schleiden (3).

Plate 19. *Wolffia papulifera* Thompson, specimens in bloom: arrows indicate flowering specimens.

All from photographs by F. J. Barham, August 10, 1927. Magnification, 11 diameters.



SAEGER: FLOWERING OF LEMNACEAE



SAEGER: FLOWERING OF LEMNACEAE



SAEGER: FLOWERING OF LEMNACEAE

Pilacre faginea proves to be a heterothallic fungus

ANGIE M. BECKWITH

In their paper, 'The Life History of *Pilacre faginea* (Fr.) B. & Br.,¹ Shear and Dodge made the statement incidentally that this fungus developed basidia in certain cultures which were presumed to be single spore cultures. Their statement was based on culture work done by the writer. They pointed out, however, that some of the cultures remained sterile, producing only conidia. With this in mind, they later suggested to the writer that further work should be done, as there appeared to be evidence that the cultures which had fruited may have contained two strains. The morphology of the conidial and basidial stages has been described in the paper referred to. The writer has recently proved that single spore cultures do not develop basidia. They are produced only when two strains of opposite sex are grown together. Due to the small size of the spores and the slowness of germination, great care is necessary to avoid the possibility of an ungerminated spore being carried into the culture with the germinating one and later producing a mycelium.

Basidiospores from a specimen on the bark of dead sycamore were plated out and single germinating spores transferred to corn meal agar slants on November 23, 1926. Five single basidiospore cultures, labelled 1, 2, 3, 4, and 5, were thus obtained. None of these monosporous cultures ever produced basidiocarps, nor did any of the numerous subcultures made from them. At least five tubes each were made of all possible combinations of these five haplonts, and fifteen cultures each of the combinations 1+2, 1+5, and 2+5. The result of these cultures was that all combinations with 1 produced basidiocarps, but all other combinations had only conidia.

From the behavior of these cultures, it seems evident that the fungus is heterothallic, mycelium no. 1 being regarded as haplont A and the others as haplonts B. Since there were so few strains involved, it was deemed advisable to test more monosporous cultures. Accordingly, basidiospores from combination culture 1+2 were isolated, and six monosporous

¹ Jour. Agr. Res. 30: 407-417. 1925.

cultures made, numbered 7, 11, 12, 13, 14, and 15. These were transferred to large tubes of potato dextrose agar. Each of these cultures was combined with the monosporous cultures 1 and 2 which had been shown to be of opposite sex. In a little over two months basidiocarps were formed in all the combinations with 2 and none in the combinations with 1, indicating that cultures 7, 11, 12, 13, 14, and 15 were haplonts A. By growing monosporous strains in pairs in various combinations, it has been shown that mycelia 1, 7, 11, 12, 13, 14, and 15 are of one sex, and haplonts 2, 3, 4, and 5 are of the opposite sex, although not all the possible combinations were made. All possible combinations, however, were made between 1, 7, 11, 12, 13, 14, and 15, but they failed to produce basidiocarps, as did combinations of 2, 3, 4, and 5. For example, ten cultures of 1 with each of haplonts 2, 3, 4, and 5 gave basidiocarps, but 2, 3, 4, and 5 in any combination remained sterile. Further studies are being made, and the complete results will be published later.

BUREAU OF PLANT INDUSTRY
WASHINGTON, D. C.

The genus *Weinmannia* in northern South America

E. P. KILLIP AND A. C. SMITH

(WITH TWO TEXT FIGURES)

The genus *Weinmannia* (Cunoniaceae) is widely distributed in the mountainous regions of the New World, ranging from Mexico to Chile and Argentina, and occurring also in the West Indies, British Guiana, and Brazil. Several species likewise are found in the Old World.

In the excellent monograph by Engler (Linnaea 36:592-650. 1869-70) about twenty species are recorded from British Guiana, Venezuela, Colombia, and Ecuador. Since the publication of this, some fifteen additional species have been described from this area. Unfortunately many of these are not represented by type or authenticated material in the herbaria of the United States, and we have seen only a small portion of the collections in European herbaria. The differences between the species consist mainly in leaf characters, and, in the absence of this material, we have frequently been unable to find satisfactory points of differentiation. We have hesitated definitely to reduce species known to us only by description, and therefore, in some cases, we have merely indicated the probable relationship.

The American species of the genus seem naturally to fall into two groups, those with simple leaves and those with compound leaves. However, even this division is not wholly satisfactory, as *W. crenata*, a species which usually has one or two pairs of leaflets, occasionally has simple leaves, and on the other hand, *W. heterophylla* and *W. auriculifera*, species with the leaves normally simple and sometimes auricled at the base, occasionally have the auricles distinct to the rachis.

Among the compound-leaved species the principal groups may be differentiated by the leaves being 1- to 3-jugate or 3- to 12-jugate, by the presence or absence of an indument on the ovary and capsule, and by the texture of the leaves.

The herbaria in which specimens we have examined are deposited are indicated thus: Arnold Arboretum (A); Botanischer Garten, Berlin (B); Gray Herbarium of Harvard University (G); U.S. National Herbarium (N); New York Botanical Garden (Y).

KEY TO SPECIES

- A. Leaves simple, auricled, or once-jugate (the lateral leaflets always much reduced when present).
 Leaf blades less than 3 cm. long.
 Habit compact; leaves rounded or subcordate at the base; racemes more than 2 cm. long with fascicles scattered along most of the length.....
 1. *W. Karsteniana*.
 Habit lax; leaves attenuate to the sessile base; racemes less than 2 cm. long with fascicles clustered near the apex.....
 2. *W. laxiramea*.
 Leaf blades 4–12 cm. long.
 Leaves usually obovate, obtuse or subobtusate at apex, abruptly attenuate at base.
 Petioles short (less than 5 mm. long); leaves glabrous above; racemes not branched.....
 3. *W. calothyrsa*.
 Petioles 8–10 mm. long; leaves pilose above; racemes branched.....
 4. *W. Lehmannii*.
 Leaves ovate or ovate-oblong.
 Leaves often auricled at base or once-jugate.
 Racemes at anthesis not more than 1 cm. wide; petioles of the jugate leaves with wings narrow or lacking.....
 5. *W. auriculifera*.
 Racemes at anthesis about 2 cm. wide; petioles of the jugate leaves broadly winged (wings about 3 mm. wide).....
 6. *W. heterophylla*.
 Leaves always simple.
 Ovary and capsule pilose.....
 7. *W. caucana*.
 Ovary and capsule glabrous.
 Upper surface of leaves hirsutulous.
 Leaves oblong or ovate-oblong, not more than 4 cm. long and 3 cm. wide.....
 8. *W. Rollottii*.
 Leaves broadly ovate, 5–7 cm. long, about 4 cm. wide.....
 9. *W. latifolia*.
 Upper surface of leaves glabrous.
 Leaves 2.5–3.5 cm. long.....
 10. *W. elliptica*.
 Leaves 5–12 cm. long.
 Nodes of the branchlets much enlarged; leaves subsessile; fascicles crowded on the racemes (about 7 per cm.).....
 11. *W. macrophylla*.
 Nodes of the branchlets scarcely enlarged; leaves distinctly petiolate; fascicles scattered on the racemes (about 4 per cm.).....
 12. *W. Balbisiana*.
 B. Leaves compound, the leaflets never reduced to auricles (leaves occasionally simple in no. 13).
 Leaves 1–3-jugate.
 Racemes 6–12 cm. long; leaves more than 4 cm. long; leaflets more than 2 cm. long.....
 13. *W. crenata*.
 Racemes 1–5 cm. long; leaves less than 3 cm. long; leaflets less than 1.5 cm. long.
 Terminal leaflet (if present) about equal to the lateral ones; racemes (including peduncles) not exceeding 2 cm. in length; calyx lobes 1.5–1.8 mm. long.
 Leaves 2–2.5 cm. long; leaflets 1–1.5 cm. long; racemes cylindric, 1.5–2 cm. long; styles less than 1 mm. long.....
 14. *W. guyanensis*.
 Leaves .5–1.5 cm. long; leaflets 6–9 mm. long; racemes subcapitate, about 1 cm. long; styles about 1.5 mm. long.....
 15. *W. microphylla*.
 Terminal leaflet larger than the lateral ones; racemes (including peduncles) 4–5 cm. long; calyx lobes 1–1.2 mm. long.....
 16. *W. stenocarpa*.
 Leaves 3–12-jugate.
 Ovary and capsule glabrous (rarely faintly pilosulous).
 Leaflets subcoriaceous, flattened when dried.

- Leaflets crenate only towards the apex (crenations 1 to 3 per side), 4 to 8 mm. long.....17. *W. fagaroides*.
- Leaflets crenate or serrate along the entire margin (or at least with the crenations more than 3 per side).
Leaves pilose above; margins of the leaflets tightly revolute....
18. *W. vegasana*.
- Leaves glabrous above; margins of the leaflets not revolute.
Terminal leaflet nearly twice as large as the lateral ones (about 5 cm. long).....19. *W. platyptera*.
- Terminal leaflet equaling the others or only slightly larger (less than 4 cm. long).
Leaves, including petioles, averaging less than 3 cm. long; petioles less than 4 mm. long; leaflets crowded (wings 5 mm. long or less).....20. *W. venezuelensis*.
- Leaves more than 3 cm. long; petioles at least 4 mm. long; leaflets separated (wings 6-13 mm. long).
Petiole invariably winged (sometimes narrowly and only in upper part).....21. *W. caripensis*.
- Petiole without wings.
Pedicels about 2 mm. long (occasionally 2.5 mm.).
Floral leaves much reduced, often simple; main leaves with leaflets 2-3 cm. long, the wings 6-12 mm. long....
22. *W. descendens*.
- Floral leaves not much reduced; main leaves with leaflets 1-2 cm. long, the wings rarely exceeding 6 mm. in length.....23. *W. Stuebelii*.
- Pedicels 3 mm. long or more; leaflets 7-11 pairs.....
24. *W. multijuga*.
- Leaflets thick-coriaceous or fleshy, becoming sulcate when dried.
Wings between the leaflets always present.
Racemes less than 5 cm. long; leaflets less than 1 cm. long, attenuate at base.....25. *W. Mariquitae*.
- Racemes 6-10 cm. long; leaflets 1-2 cm. long, subacute at base.
26. *W. Engleriana*.
- Wings between the leaflets lacking or present only between the upper leaflets.
Stipules small; wings between the leaflets broadly semi-oblong, attenuate towards the base, lacking between the inferior leaflets.....
27. *W. sulcata*.
- Stipules large (about 1 cm. across); wings between the leaflets rarely present (when present very narrowly semi-oblong). 28. *W. Trianae*.
- Ovary and capsule uniformly pilose.
Leaflets less than 8 mm. long, the margins entire, revolute.....
29. *W. tomentosa*.
- Leaflets more than 8 mm. long, the margins serrate or crenate, not revolute (or barely so).
Both sides of the leaflets pilose (rarely glabrous above).
Leaflets more than 1 cm. broad.....30. *W. pubescens*.
- Leaflets less than 1 cm. broad.....30a. *W. pubescens popayanensis*.
- Both sides of the leaflets glabrous, or faintly pilose on the larger nerves.....31. *W. Lansbergiana*.

1. *W. KARSTENIANA* Szyszy. Oesterr. Bot. Zeitschr. 40: 41. 1890. An excellently marked species which seems endemic to the mountains of western Venezuela. It is readily identified by its small subcordate leaves and by its compact habit.

VENEZUELA: Trujillo: Páramo de Jabón, 3100 m., *Jahn* 94 (N).

2. *W. laxiramea*, sp. nov. Small tree or shrub with branchlets elongated, lax; branchlets and racemes ferruginous-tomentose with crisp spreading hairs about .4 mm. long; internodes 2–4.5 cm. long; stipules somewhat semielliptic, about 2 mm. in diameter, deciduous; leaves simple, ovate or nearly obovate, 1.5–2.8 cm. long, .8–1.8 cm. wide, rounded at apex, attenuate and practically sessile at base, glabrous throughout, coriaceous, lustrous, serrate in the upper one-half or two-thirds, the serrations 3–6 per side (about 3 per cm.), acutish, callous-thickened at apex, the veins arcuate-ascending, ramifying near the margin, 4–6 per side; racemes axillary or terminal, in pairs, 1.5–2 cm. long; fascicles clustered near the apex, 2–6-flowered; bractlets about .5 mm. in diameter; pedicels 2.5–3.8 mm. long, sparsely strigulose; calyx-lobes lance-ovate, blunt, glabrous, 1.6–1.9 mm. long; petals red, oblong, rounded, about 2 mm. long; stamens 3–3.8 mm. long; ovary ovoid, 1–1.4 mm. long, glabrous; styles 1.6–2.4 mm. long.

Type, *Tate 395*, collected Nov. 24, 1927, on summit of Mt. Roraima, British Guiana, and deposited in the herbarium of the New York Botanical Garden. Another collection from the same locality is: *Jenman 327* (N).

A well marked species, apparently endemic to Mt. Roraima, distinguished from *W. Karsteniana* Syzsy. by its lax habit and its attenuate-based leaves.

3. *W. CALOTHYRSA* Diels, Bot. Jahrb. 37: 413. 1906. This species is characterized by very thick obovate leaves. It apparently is confined to the Popayán region of Colombia.

COLOMBIA: Dept. El Cauca: Popayán, 1500–2000 m., *Lehmann 5418* (B, type), *Lehmann B. T. 1064* (Y), *B. T. 1065* (Y), *B. T. 1066* (Y). Río Ortega, north of Tambo, 2000–2100 m., *Pennell & Killip 8055* (N, Y).

4. *W. LEHMANNII* Hieron. Bot. Jahrb. 20: Beibl. 49: 21. 1895. We have not seen specimens of this species, concerning which Hieronymus writes: 'foliis supra subtusque parce hirtopilosis' and 'inflorescentia composita, terminale, trifida, ramis bifidis vel trifidis; pseudoracemis binis vel ternis.' These points and the longer petioles, seem to distinguish it from *W. calothyrsa*.

Type from Colombia: Antioquia, *Lehmann 7433*.

5. *W. AURICULIFERA* Hieron. Bot. Jahrb. 20: Beibl. 49: 22. 1895. A species with variable coriaceous leaves and numerous slender spikes, easily distinguished from allied species.

COLOMBIA: El Cauca: Highlands of Popayán, 1600–1800 m. *Lehmann* 7710 (B, type; N), *Lehmann* B. T. 1063 (Y), B. T. 1264 (Y). Río Sucio, west of Popayán, 1900 m., *Pennell & Killip* 8198 (N).

6. *W. HETEROPHYLLA* H. B. K. Nov. Gen. & Sp. 6: 53. pl. 522. 1823. A species which suggests *W. auriculifera* in its once-jugate or auriculate leaves, but which differs in its thicker racemes and broadly winged petioles.

Type from Colombia: Cundinamarca, near Bogotá.

7. *W. CAUCANA* Killip, Journ. Washington Acad. Sci. 16: 568. 1926. This is the only species in the simple-leaved group having pilose ovaries.

COLOMBIA: El Cauca: Morales, 1680–1720 m., *Pennell & Killip* 8306 (N, type). Río Piendamó north of Popayán, 1700 m., *Pennell & Killip* 8286 (N, Y).

8. *W. ROLLOTTII* Killip, Journ. Washington Acad. Sci. 16: 568. 1926. The leaves of this species are smaller than those of its immediate relatives and in addition are hirtellous above.

COLOMBIA: Cundinamarca: Páramo de Guasca, *Ariste Joseph* 4476 (N, type). Tolima: Higher reaches of the Quindío, 2400 m., *Dawe* 802 (Y). El Cauca: Las Escaleretas, Moras Valley, Río Paez basin, 2800 m., *Pittier* 1378 (N); West Andes of Popayán, 2800 m., *Lehmann* 8536 (Y). The *Lehmann* specimen, consisting only of inflorescence and floral leaves, may not belong here.

9. *W. LATIFOLIA* Presl, Rel. Haenk. 2: 51. 1831.—*W. rugosa* Benth. Pl. Hartw. 132. 1844. We have seen no specimen of this. Engler considers *W. rugosa*, based on a Hartweg plant from Loja, a synonym of *W. latifolia*. From the drawing of a single leaf (Martius, Fl. Bras. 14²: pl. 38, f. 1.), the blades are evidently much larger and proportionately broader than in the case of other species of this immediate relationship.

10. *W. ELLIPTICA* H. B. K. Nov. Gen. & Sp. 6: 50. 1823. The single Humboldt specimen was collected near Loja, Ecuador. Engler has modified the description to include collections from British Guiana and Venezuela which probably are better referable to *W. Balbisiana*. True *W. elliptica* is apparently a species with small subsessile leaves.

11. *W. MACROPHYLLA* H. B. K. Nov. Gen. & Sp. 6: 51. 1823. The largest leaved species in our range, its size emphasized by

the large nodes of the branchlets and the large numerous stipules.

ECUADOR: Loja: Between La Toma and Loja, 1800–2600 m., *Hitchcock* 21435 (N, Y). Without locality, *Jameson* (U. S. N. H. 700,163).

12. *W. BALBISIANA* H. B. K. Nov. Gen. & Sp. 6: 51. *pl.* 520. 1823.—*W. ovata* Cav.' H. B. K. Nov. Gen. & Sp. 6: 52. 1823. *W. Kunthiana* D. Don, Edinb. Phil. Jour. 9: 85. 1830. *W. lamprophylla* Diels, Bot. Jahrb. 37: 412. 1906. The specimens cited below appear to represent a single species, although they show a certain amount of variation in shape and texture of the leaves and in the proportionate length of the racemes. Although we have not seen type material of *W. Balbisiana*, we are unable to find any important difference between the excellent drawing and diagnosis of the plant given by Kunth and the type material of *W. lamprophylla*. Kunth's description of a Humboldt plant collected at Bogotá which he referred to *W. ovata* Cav., and which was later described as *W. Kunthiana*, fails to point out satisfactory features of differentiation from *W. Balbisiana*. *W. ovata* Cav. is a Peruvian plant of which we have seen no authentic material. It may possibly be conspecific with *W. Balbisiana*, although if Pennell's 14099 from Cuzco, Peru, is true *W. ovata*, that species is quite distinct in having very thick leaves with strongly reticulate veins, and capsules fully twice as large as the Colombian specimens.

W. laurina H. B. K. apparently is this relationship. The type locality is not given, and it may not be within our area. We have seen no specimens which agree with the description.

VENEZUELA: Mérida: *Moritz* 1141 (N). Páramo de Quirorá, 2000 m., *Jahn* 712 (N, Y). Páramo La Trampa, 2100 m., *Jahn* 996 (N, Y). Páramo del Morro, 2700 m., *Jahn* 1074 (N, Y).—COLOMBIA: Norte de Santander: Between Mutiscua and Pamplona, 2700 m., *Killip & Smith* 19766 (A, G, N, Y). El Cauca: Andes west of Popayán, 2800–3200 m., *Lehmann* 5416 (B, type of *W. lamprophylla*; N, photo). La Gallera, 1800 m., *Killip* 7898 (N, Y).—ECUADOR: without locality, *Jameson* (U. S. N. H. 534,631).

13. *W. CRENATA* Presl, Rel. Haenk. 2: 51. 1831.—? *W. sorbifolia* H. B. K. Nov. Gen. & Sp. 6: 57. 1823.—? *W. Spruceana* Engl. *Linnaea* 36: 607. 1869–70. The specimens cited below

show a certain amount of variation in the cutting of the leaves and the shape of the leaflets. In a few of the specimens simple leaves are found, in others there are three pairs of leaflets. The rachis usually is rather broadly winged, although in some specimens it is scarcely winged at all. The shape of the leaflets varies from narrowly elliptic-oblong to broadly ovate. About half the specimens cited have glabrous ovaries; in the others the ovaries and capsules are faintly or densely pilose. It is doubtful if more than one species is represented, although some of the Santander specimens suggest *W. Balbisiana*. It seems unlikely that a species as common as this appears to be in Colombia would have been overlooked by Humboldt, and possibly it was described under the name of *W. sorbifolia*. However, certain details in the description of that species, such as serrate leaflets with the mid-nerves pilosulous beneath, do not agree at all with material which we have seen. The type locality of *W. sorbifolia* is given merely as 'Nova Granata'.

W. Spruceana, known to us only by description, is perhaps a form of this.

VENEZUELA: Mérida: Páramo de Canaguá, 1900 m., *Jahn* 914 (N), 915 (N). Tachira: Guaraqué, 1700 m., *Jahn* 93 (N).—COLOMBIA: Norte de Santander: Pamplona, 2200 m., *Killip & Smith* 19797 (A, G, N, Y). Toledo, 1800 m., *Killip & Smith* 20050 (A, G, N, Y). Santander: Las Vegas, 2600 m., *Killip & Smith* 16109 (A, G, N, Y). Suratá, 2200 m., *Killip & Smith* 16745 (A, G, N, Y). La Baja, 2700 m., *Killip & Smith* 18041 (A, G, N, Y). Charta, 2000 m., *Killip & Smith* 18887 (A, G, N, Y), 19305 (A, G, N, Y). Tona, 2000 m., *Killip & Smith* 19461 (A, G, N, Y), 19516, (A, G, N, Y). Cundinamarca: Chipaqué, 2600 m., *André* 909 (Y). Bogota, *Ariste Joseph* B107 (N). Páramo de Guasca, *Ariste Joseph* B108 (N). Huila: Neiva, 1300 m., *Rusby & Pennell* 1057 (N, Y), 544 (Y). Antioquia: Titiribi, *Toro* 349 (Y). El Cauca: Pedregal, 1600 m., *Lehmann* 6668 (N).—ECUADOR: Loja: Las Juntas, *Lehmann* 4980 (N, Y), cited by Hieronymus as *W. cinerea* R. & P. (Bot. Jahrb. 20: Beibl. 49: 24).

14. *W. GUYANENSIS* Klotzsch, ex Engler in *Linnaea* 36: 605. 1869–70. A well marked species apparently endemic to Mt. Roraima. The leaflets bear a strong resemblance to the simple leaves of *W. laxiramea* K. & S., which has possibly been confused with it in many herbaria.

BRITISH GUIANA: Mt. Roraima, summit, *Tate* 387 (Y).

15. *W. MICROPHYLLA* H. B. K. Nov. Gen. & Sp. 6: 54. *pl.* 523. 1823.—? *W. cochensis* Hieron. Bot. Jahrb. 21: 310. 1895. A species ranging from southern Ecuador to the Cauca Valley of Colombia, distinguished by its small leaflets and short racemes, the flowers of which are clustered near the apex.

Hieronymus likens *W. cochensis* to *W. fagaroides* H. B. K., but we are not able to distinguish it from *W. microphylla*. We have seen none of the numerous Stuebel collections cited as this by Hieronymus.

COLOMBIA: Cauca: Páramo de Buena Vista, Huila Group, Central Cordillera, 3000–3600 m., *Pittier* 1165 (N, Y). Páramo Las Delicias, Central Andes of Popayán, 2800–3600 m., *Lehmann* B. T. 500 (Y).—ECUADOR: Loja, 2800–3400 m., *André* K1008 (Y); *Lehmann* 4978 (N).

16. *W. stenocarpa* sp. nov. Shrub or small tree; branchlets slender, sulcate, blackish-tomentose at extremities, the older parts glabrous; stipules soon deciduous; petioles 3–5 mm. long, ferruginous-tomentose; leaves compound, 1.3–2 cm. long., .8–1.2 cm. wide, 1–3-jugate; leaflets glabrous, bright green above, slightly paler beneath, crenate above middle, the terminal leaflet ovate or rhombic-ovate, 8–15 mm. long, 4–8 mm. wide, obtuse at apex, acute and sessile at base, sometimes auricled, the crenations about 5 per side, the lateral leaflets similar and smaller, 4–8 mm. long, 3–4 mm. wide, sessile or merged into the winged rachis; racemes axillary in pairs, 4–5 cm. long (including peduncles), the flowers in clusters of 2–4 (sometimes solitary?), the pedicels filiform, about 3 mm. long, minutely strigose; calyx lobes ovate, 1–1.2 mm. long, acute, glabrous; stamens about 2.5 mm. long; capsule narrowly oblong, about 3.5 mm. long, 1.3 mm. in diameter, glabrous; styles 1–1.5 mm long.

Type, *Hitchcock* 21518A, collected Sept. 7, 1923, between San Lucas and Oña, Province Loja, Ecuador, alt. 2200–3100 m., and deposited in the U. S. National Herbarium (no. 1,195,637).

The size of the terminal leaflet and the elongate racemes readily differentiate *W. stenocarpa* from the two preceding species. From *W. crenata*, which it resembles in the general form of the leaves, it is distinguished by the leaves being much smaller and the racemes, although fully developed, much shorter.

17. *W. FAGAROIDES* H. B. K. Nov. Gen. & Sp. 6: 54. 1823.

A widespread Andean species distinguished by its small leaflets, of which there are 3-8 pairs.

VENEZUELA: Mérida: Páramo Quirorá, 2000 m., *Jahn 711* (N, Y).—COLOMBIA: Norte de Santander: Páramo de Santurbán, towards Mutiscua, 3900 m., *Killip & Smith 19590* (A, G, N, Y). Páramo de Romeral, 4000 m., *Killip & Smith 18656* (A, G, N, Y). Santander: Páramo de las Vegas, 3500 m., *Killip & Smith 15737* (A, G, N, Y). Western slope of Páramo Rico, 3500 m.,



Fig. 1. *Weinmannia fagaroides* from the eastern slope of the Páramo de Santurbán, Colombia. (*Killip & Smith 19590*). This dwarfed tree is a characteristic plant of the upper temperate zone in Colombia.

Killip & Smith 17747 (A, G, N, Y). Páramo de Santurbán, near Vetas, 3500 m. *Killip & Smith 17930* (A, G, N, Y). Cundinamarca: Eastern Páramos of Guasca, towards Gacheta, *Ariste Joseph B109* (N). Caldas: Cerro Tatamá, 3400 m., *Pennell 10537* (N).—ECUADOR: Moridino, *Lehmann 4981* (N, Y). Azuay: Vicinity of Cumbe, *Rose 22979* (N, Y). Cuenca, 3000 m., *Lehmann 6595* (N). Loja: Between San Lucas and Oña, 2200-3100 m., *Hitchcock 21518* (N, Y).

18. *W. vegasana* sp. nov. Tree 5 to 6 meters high; branchlets, racemes, and petioles ferruginous- or grayish-tomentose (becoming black), the hairs 2-.8 mm. long; petioles 3-5 mm. long; leaves 4-6-jugate, 3-5 cm. long, 1.5-2 cm. wide, the rachis short-tomentose above, hirsute below, especially at the nodes (hairs pale, .5-.8 mm. long); leaflets ovate or oblong-ovate (terminal one slightly larger), 8-15 mm. long, 5-7 mm. wide, tightly revolute at margin, and shallowly crenate in upper half (crenations about 1.6 mm. apart), finely pilosulous above (hairs .3 mm. long, about 8 per sq. mm.), below pilose on the mid- and some of the secondary-nerves, otherwise glabrous or very minutely pilosulous, the axils of the teeth sometimes tufted-pilose; wings semi-ovate or semi-obovate, pubescent as the leaflets, 4-7 mm. long, 1-2 broad; racemes numerous, in pairs at apices of short branches, 6-9 cm. long, the floral leaves resembling the others but reduced to 1-2 cm. long, 2-3-jugate; fascicles about 4 per cm., 3-6-flowered; bractlets ovate-oblong, about .8 mm. long, deciduous, pubescent; pedicels stout (about .3 mm. in diameter), 1-2 mm. long, sometimes up to 3 mm., loosely strigose with pale short hairs; calyx-lobes ovate, 1-1.3 mm. long, acutish, pubescent with spreading hairs especially at the apex; petals oblong, about 1.7 mm. long, usually short-ciliate (cilia 12-16 per mm.) reddish; stamens slender, about 3.8 mm. long; ovary ovoid, about 1 mm. long, glabrous, or faintly pilose towards the apex; styles 1.8-2.4 mm. long, strigose with pale short hairs (about .1 mm. long) on lower half, especially on inner surfaces.

Type, *Killip & Smith 15840*, collected Dec. 21, 1926, mountains east of Las Vegas, Dept. Santander, Colombia, alt. 3000-3300 m., and deposited in the herbarium of the New York Botanical Garden (duplicates A, G, N).

A well-marked species distinguished by the pilose upper surface of its leaflets and their tightly revolute margins.

19. *W. PLATYPTERA* Diels, Bot. Jahrb. 40: Beibl. 91: 45. 1907. Concerning this species, of which we have seen no specimens, Diels writes: 'Species foliis inaequalibus *W. lentiscifolia* Presl peruvianae similis, sed alis majoribus atque pseudo-racemis multo longioribus floribundis recedit.' With the aid of the description we separate this from other species of our region on the size of its terminal leaflet, which is much larger than the lateral leaflets.

ECUADOR: 'in silvis subtropicis secus flum. Pilaton et ad Pangoa (Sodiho n. 442—Herb. Berol.)'

20. *W. venezuelensis* sp. nov. Shrub or small tree, the branches dark gray, glabrous, the branchlets densely rufo-hirsute; stipules subreniform, about 4 mm. long, 5 mm. wide, membranous, sparingly hirtellous or glabrous, soon deciduous; petioles 2-4 mm. long, wingless or rarely obscurely winged, densely hirsute; leaves 1.5-3.5 cm. long, 1-2 cm. wide, hirsutulous along rachis especially at articulations, glabrous above, glabrous or sparingly hirsutulous on nerves beneath, coriaceous, flat or occasionally the nerves impressed above, 3-6-jugate, the leaflets ovate, oblong, obovate, or subrhombic, 6-10 mm. long, 3-6 mm. wide (terminal subequal to lateral), obtuse or occasionally subacute at apex, acute at base, serrate with 4-7 (rarely 3) serrations to a side, penninerved (midnerves prominent beneath, the lateral nerves 5-8 to a side, often obscure), the rachis winged, the wings semi-ob lanceolate, 3-5 mm. long, .7-1.5 mm. (rarely up to 2 mm.) wide; racemes terminal in pairs, 2-5 cm. long (including peduncle which is up to 1 cm. long), about 1 cm. wide at anthesis, up to 1.5 cm. wide in fruit, the fascicles crowded on the raceme, 5-8-flowered, the pedicels 2-2.5 mm. long, hirtellous; calyx-lobes ovate-lanceolate, .8-1.2 mm. long, glabrous or minutely hirtellous towards apex; petals obovate, about 1 mm. long, .8 mm. wide, rounded; filaments 1.3-1.5 mm. long, anthers globose, about .4 mm. in diameter; ovary lance-ovoid, glabrous; capsule ovoid, 2.5 mm. long, the persistent styles about 2 mm. long.

Type, *Pittier 6250*, collected May 24, 25, 1913, in upper belt of Pico de Naiguatá, Miranda, Venezuela, alt. 2400-2765 m., and deposited in the U. S. National Herbarium (no. 601,985), in fruit; duplicate Y. Description of the flowers is based upon *Kuntze 1652* from Silla de Caracas, Venezuela (Y). Other specimens are: BRITISH GUIANA: Mt. Roraima, *Tate 383* (Y), *Jenman 321* (N).—VENEZUELA: Sucre: Cerro de Turumiquiré, 2925 m., *Tate 205* (N), *206* (N). Federal District: Silla de Caracas, 2500 m., *Jahn 198* (N); *Pittier 8349* (N). Falcón: Paraguana Peninsular, *Curran & Haman 688* (N, Y). Mérida: Páramo del Molino, 2800 m., *Jahn 938* (N), *938a* (N).

This species is intermediate between *W. fagaroides* and *W. caripensis*. The leaves are much smaller than in *W. caripensis*, but the leaflets have several more serrations to a side than in *W. fagaroides*. The inflorescence is more compact than in either of these.

The shape and size of the leaves of this species agree with the description of *W. Lansbergiana*, but the ovaries of that species have a distinctly cinerous-pilose indument which per-

sists on the capsules. In Pittier's 8349, in flower only, there are a few hairs towards the tips of the ovaries, but it is doubtful if these persist in fruit.

21. *W. CARIPENSIS* H. B. K. Nov. Gen. & Sp. 6: 58. 1823. — *W. glabra caripensis* Engl. Linnaea 36: 614. 1869–70. *W. nitida* Hieron. Bot. Jahrb. 20: Beibl. 49: 23. 1895. *W. nervosa* Killip, Jour. Washington Acad. Sci. 16: 569. 1926.

VENEZUELA: Federal District: Coastal Range, 1900 m., Pittier 8128 (N). Aragua: Colonia Tovar, 2000 m., Fendler 518 (N, Y); Allart 481 (N, Y); Pittier 9253 (N, Y). Mérida: Selva de Tafayés, 1800 m., Jahn 538 (N). Páramo Quirorá, 2000 m., Jahn 702 (N).—COLOMBIA: Magdalena: Santa Marta, 1500 m., H. H. Smith 1944 (Y), 1743 (N, type of *W. nervosa*; Y). Norte de Santander: La Isla, 2300 m., Killip & Smith 19809 (A, G, N, Y). Santander: Mesa de los Santos, 1500 m., Killip & Smith 15105 (A, G, N, Y). Las Vegas, 2800 m., Killip & Smith 15897 (A, G, N, Y), 15989 (A, G, N, Y). Cundinamarca: Fusagasugá, 2300 m., Triana (Y). Antioquia: Pingura, 1500 m., Lehmann 4635 (N, Y), type collection of *W. nitida*).

All of these specimens are characterized by slender spikes with flowers short-pedicellate. The petioles are noticeably longer than those of *W. venezuelensis* and are winged. The leaflets show considerable variation in outline, ranging from elliptic-lanceolate to broadly ovate. The terminal leaflet in nearly every case is acute, but the lateral leaflets vary from acute to strongly obtuse. The venation is obscure in the greater part of these specimens, although in the case of one Santa Marta plant (H. H. Smith 1743) and two of the Venezuelan plants it appears as a conspicuous pale network on the upper surface.

W. caripensis may be merely a form of the West Indian *W. pinnata* L., as considered by some writers. However, all of our Jamaican material of this has the fascicles more loosely arranged, the flowers longer-pedicelled, and capsules nearly twice as long.

In the type specimen of *W. nitida* the pedicels are extremely short, but no constant differences are found to separate it.

22. *W. DESCENDENS* Diels, Bot. Jahrb. 37: 414. 1906.

Type locality: PERU: Loreto: Moyobomba, 900 m., Weberbauer 4572 (B, type; N, photo).—ECUADOR: Loja: Between

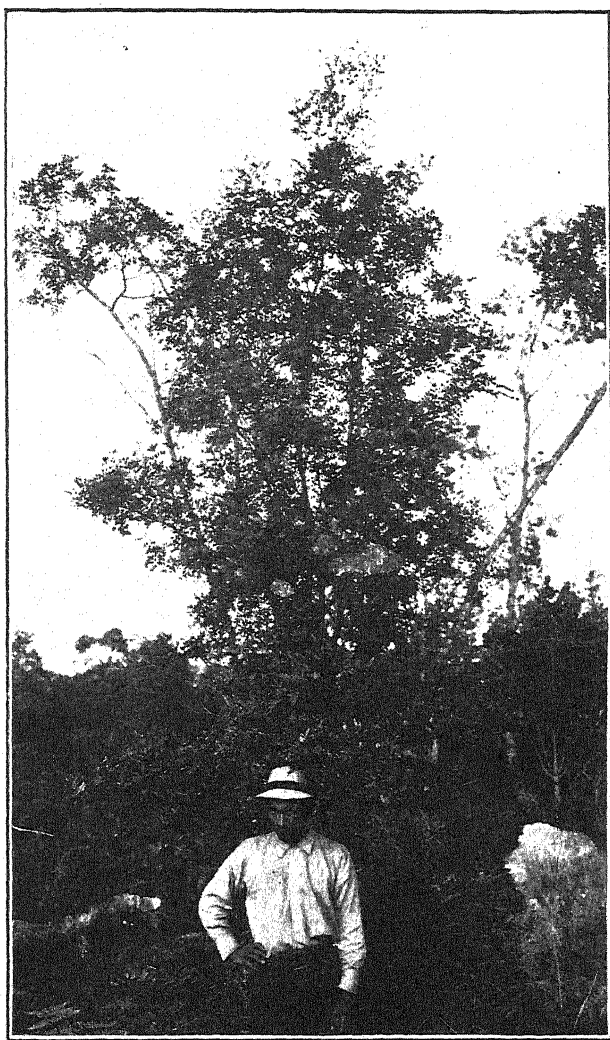


Fig. 2. *Weinmannia caripensis* from the Mesa de los Santos, Colombia. (Killip & Smith 15105). This is one of the commoner species of *Weinmannia* at middle elevation.

El Tambo and La Toma, 1000-2200 m., *Hitchcock 21365* (N, Y).

This and the following species are characterized by their wingless petioles and slender spikes.

23. W. STUEBELII Hieron. Bot. Jahrb. 21: 309. 1905.

COLOMBIA: Santander: La Baja, 3000 m., *Killip & Smith 18042* (A, G, N, Y).—ECUADOR: 'Andes', 2700 m., *Jameson 131* (Y).

In the Colombian specimen the indument on the upper surface of the leaflets is more evident.

24. W. *multijuga* sp. nov. Shrub or small tree, 2.5-6 m. high; branchlets rufo-hirsutulous, at length glabrescent; stipules rounded, reniform, 4-5 mm. long, 5-6 mm. wide, glabrous, hirtellous near margin; petioles 8-20 mm. long, stout, wingless, terete, densely hirsute-tomentose; leaves 7-16 cm. long, 3-6 cm. wide, pilosulous along rachis especially at articulations, 7-11-jugate (rarely 5-), the leaflets coriaceous, lustrous and conspicuously reticulate-veined above, slightly paler beneath, minutely tomentellous on midnerve above, sparingly hirtellous on midnerve beneath, crenate-serrate or sharply serrate nearly to base (serrations 9-15 to a side), the terminal leaflet ovate-elliptic, obtuse or acutish at apex, acutish at base, the lateral leaflets oblong, nearly as large as the terminal, 1.5-3 cm. long, .8-1.4 cm. wide, rounded or occasionally acutish at base, sessile, wings between the leaflets semi-oblongate, 7-10 mm. long, 2-5 mm. wide, glabrous; racemes terminal in pairs, 8-13 cm. long, 1.5-2 cm. wide in fruit; peduncles 1.5-2 cm. long; fascicles 2-6-flowered, the bractlets cordate-ovate, about 1 mm. long, the pedicels slender, 3-6 mm. long, finely strigose; calyx-lobes ovate about 1 mm. long, obtuse, glabrous, sometimes puberulous at apex; stamens 2.5-3.5 mm. long; ovary globose-ovoid, glabrous; capsule broadly ovoid, 2.8-3.5 mm. long, styles persistent, 1.5-2 mm. long; seeds lance-ovoid, about 1 mm. long, with 30-50 long crispate hairs.

Type, *Killip & Smith 20597*, collected Mar. 12, 1927, on the eastern slope of Páramo del Hatíco, between Toledo and Pamplona, Dept. Norte de Santander, Colombia, alt. 2900 m., and deposited in the herbarium of the New York Botanical Garden. Duplicates A, G, N. Other specimens are: VENEZUELA: Mérida: Selva de Tafayés, 2000 m., *Jahn 537* (N, Y).—COLOMBIA: Norte de Santander: between Pamplona and Toledo, 2800 m., *Killip & Smith 19907* (A, G, N, Y), *20637* (A, G, N, Y). Santander: Las Vegas, 2800 m., *Killip & Smith 16134* (A, G, N, Y).

The numerous leaflets and long pedicels distinguish this species from its near relatives.

25. *W. MARIQUITAE* Szyszy. Oesterr. Botan. Zeitschr. 40: 41. 1890. We have not seen a specimen of this, which the author compares with *W. sulcata* Engl. From this it seems to be differentiated by the invariable presence of wings, more slender racemes, and smaller leaflets. The type is from Colombia, 'prov. Mariquitae, Boqueron du Tolima, alt. 4000 m., *Linden* 932, in Herb. Mus. pal. Vind.'

26. *W. ENGLERIANA* Hieron. Bot. Jahrb. 20: Beibl. 49: 24. 1895.—? *W. hirtella* H. B. K. Nov. Gen. & Sp. 6: 56. 1823. *W. guanacasana* Hieron. Bot. Jahrb. 20: Beibl. 49: 25. 1895. We have not seen the type specimen of *W. hirtella*, or any of the collections cited as such by Engler or Hieronymus. The description applies well to type material of *W. Engleriana*.

W. guanacasana surely is conspecific with *W. Engleriana*. In discussing its relationship Hieronymus writes: 'Species *W. Englerianae* Hieron. affinis, differt foliis 3-7-jugis, brevius petiolatis, foliolis minus crassis subplanis vel leviter sulcatis et argutius serratis, allis interfoliolaribus superioribus paulo latioribus, floribus paulo minoribus, brevius pedicellatis.' Careful comparison of specimens of the type collections convinces us that the above differences, which exist in a minor and overlapping degree, are purely individual and not of specific value.

COLOMBIA: Cundinamarca: Verjón, *Ariste Joseph* A95 (N). El Cauca: Río Lopez, 2700 m., *Pittier* 1072 (N, Y). Páramo de Guanacas, 3200 m., *Lehmann* 5632 (N, type collection), 6074 (N, type collection of *W. guanacasana*), 6661 (N). Páramo de Moray, 3000 m., *Lehmann* 3765 (N). Mt. Puracé 3400 m., *Pennell & Killip* 6521 (N, Y), 6525 (N, Y), 6545 (N). Mt. Pan de Azucar, *Pennell* 7033 (N).—ECUADOR: Penipe, *Mille* 63 (Y).

27. *W. SULCATA* Engler, *Linnaea* 36: 624. 1869-70. A species with the wings between the leaflets rudimentary in the lower part of the leaf, but well developed in the upper part.

Not present in our material. The type is from the Andes of Ecuador, *Spruce* 5410.

28. *W. TRIANAE* Wedd. Chlor. And. 2: 211. pl. 72. 1855. In this species the wings are all reduced to mere ridges along the rachis.

COLOMBIA: Cundinamarca: Quetamé, *Dawe* 319 (N).

29. *W. TOMENTOSA* L. f. Suppl. 227. 1763. A readily distinguished species, showing almost no variation throughout its range. It appears to bear the same relationship to the pilose-ovaryed group as *W. fagaroides* bears to those with glabrous ovaries.

VENEZUELA: Trujillo: Páramo de Zumbador, 2600 m., *Jahn* 92 (N). Mérida: Páramo Mucuchies, 3600 m., *Bellard* 53 (N).—COLOMBIA: Norte de Santander: Between Mutiscua and Pamplona, 3400 m., *Killip & Smith* 19707 (A, G, N, Y). Páramo del Hatíco, 2900 m., *Killip & Smith* 20625 (A, G, N, Y). Santander: Mountain east of Las Vegas, 3300 m., *Killip & Smith* 15833 (A, G, N, Y). Vicinity of La Baja, 3500 m., *Killip & Smith* 18037 (A, G, N, Y). Páramo de las Puentes, above La Baja, 3600 m., *Killip & Smith* 18194 (A, G, N, Y). Eastern slope of Páramo de las Coloradas, above La Baja, 3600 m., *Killip & Smith* 18392 (A, G, N, Y). Cundinamarca: Bogotá, 2900 m., *Triana* 2802 (Y); *Holton* 663 (Y); *Dawe* 147 (N); *Pennell* 2368 (N, Y). Chipaqué, 2800 m., *André* 911 (Y). San Cristóbal, *Ariste Joseph* A255 (N). Facatativá, 2700 m., *Popenoe* 1132 (N).

30. *W. PUBESCENS* H. B. K. Nov. Gen. & Sp. 6: 56. 1823.

VENEZUELA: Mérida: Páramo del Molino, 2600 m., *Jahn* 925 (N). Palmira, 2500 m., *Jahn* 536 (N).—COLOMBIA: Antioquia: Las Minitas, south of Caldas, 2300 m., *Pennell* 10935 (N, Y). Yarumal, 2000 m., *Lehmann* 7448 (Y). Santa Rosa, 2400 m., *Lehmann* 7457 (Y). Medellín, *Toro* 227 (N, Y). El Valle: El Saladito, above Cali, 1500 m., *Pittier* 753 (N). Caldas: Old Quindío Trail, 3100 m., *Killip & Hazen* 9470 (N, Y); *André* 2261 (Y). Salento, 2800 m., *Pennell* 9301 (N). El Cauca: Tacueyo, Río Palo Valley, 1800 m., *Pittier* 1048 (N, Y). Coconuco, 2400 m., *Killip* 6860 (N, Y). Río Sucio, 1900 m., *Pennell & Killip* 8194 (N). San Isidro, Puracé, 2100 m., *Pennell & Killip* 6427 (N). Morales, 1700 m., *Pennell & Killip* 8289 (N). Tolima: Río Toche, *Holton* 664 (Y).

30a. *W. pubescens popayanensis* (Hieron.) comb. nov. Described as a distinct species by Hieronymus in Bot. Jahrb. 20: Beibl. 49:26. 1895. It seems to differ from the preceding only in the narrower leaflets, a difference which examination of the type collection does not cause us to believe specific.

COLOMBIA: El Cauca: Popayán, 1500-2000 m., *Lehmann* 2084 (N, type collection).

31. *W. LANSBERGIANA* Engl. *Linnaea* 36: 628. 1869-70.

VENEZUELA: Federal District: Gálipan, *Allart* 155 (N,Y).

The leaves of this specimen are slightly broader than indicated in the description of *W. Lansbergiana*, and the indument less dense. We refer the specimen to *W. Lansbergiana* rather than to *W. caripensis*, which superficially it more closely resembles, on the base of the densely cinereous-pilose ovaries.

INDEX TO AMERICAN BOTANICAL LITERATURE

1928-1929

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Studies on the flora of northern South America—XIII. The
Tate collection from Mount Roraima and vicinity¹

H. A. GLEASON

Since its first partial exploration by Schomburgk nearly a century ago, Mount Roraima and the region about it has been known for its remarkably rich flora and high development of endemism. Although the mountain stands a comparatively short distance from the coast of British Guiana on the north and from the navigable waters of the Rio Branco on the south, access to the locality has always been a matter of considerable difficulty, and botanical exploration is still by no means complete.

After the Quelch and McConnell expeditions to the mountain in 1894 and 1898, Brown discussed the botanical history, geology, flora, and phytogeography of the region and reference to his paper is recommended for information on all of these subjects.² Since that time apparently only two botanical collections have been made from the summit. E. Ule spent seven weeks on the slopes of the mountain in December, 1909, and January, 1910, and made four ascents to its summit. His collections included a considerable number of undescribed species.

G. H. H. Tate, of the American Museum of Natural History, conducted a zoological expedition to Mount Roraima in the winter of 1927 and 1928, and the collections of botanical material which he made incidentally form the subject of this paper. These collections as received by the New York Botanical Garden include 515 numbers, of which the first 149 were made on the savannas and accompanying marshes of extreme northern Brazil, 127 on the lower slopes of Roraima below 5000 feet altitude, 153 on the upper slopes and ledges of the mountain, and 86 on the summit plateau. Notwithstanding the difficulty in preparing material, caused by the tedious transportation of supplies and the humid climate, the whole series is ample in

¹ Contributions from The New York Botanical Garden, No. 313.

² BROWN N. E. Report on two botanical collections made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. Trans. Linn. Soc. Bot. II. 6: 1-107. *pl.* 1-14. 1901.

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quantity, excellent in quality, and generally in good condition for study, and it forms a notable addition to the meager representation of this flora in American herbaria.

In identifying the collection, I have had the advantage of comparison with the older Roraima material in the herbarium of the Royal Botanic Gardens at Kew. Here are found the original sets of Schomburgk, Appun, Im Thurn, and Quelch and McConnell, including the types of the numerous species discovered by them, and an almost complete set of the later collections of Ule. I have also had for certain groups the assistance of several American specialists, including Oakes Ames (Orchidaceae), J. H. Barnhart (Lentibulariaceae), S. F. Blake (Carduaceae, Polygalaceae), N. L. Britton (Cyperaceae, Mimosaceae), Carl Epling (Labiatae), A. S. Hitchcock (Gramineae), E. P. Killip (Boraginaceae, *Passiflora*, *Weinmannia*, *Viburnum*), W. R. Maxon (Pteridophyta), F. W. Pennell (Scrophulariaceae), B. L. Robinson (Eupatorieae), P. A. Rydberg (Carduaceae), A. C. Smith (Pteridophyta, *Weinmannia*, *Viburnum*), L. B. Smith (Bromeliaceae), P. C. Standley (*Ficus*, Rubiaceae), and Percy Wilson (*Phytolacca*, *Jussiaea*).

Lack of space prevents the printing of a complete list of the collection, which includes more than four hundred species, and I give below merely diagnoses of several hitherto undescribed species, a few nomenclatorial changes, and occasional informative notes. These have in several cases been prepared by one or another of the botanists named above. The article concludes with a list of additions to the known flora of the higher altitudes of Mount Roraima.

1. NEW OR NOTEWORTHY SPECIES

DICHROMENA sp. A species apparently without a name; it was distributed in the Spruce collections as *Psilocarya monostachya*. On mud where water is receding, Limao, extreme northern Brazil: *no.* 73.

Xyris decussata Gleason, n. sp. Section NEMATOPUS: caulescent, the strongly distichous leaves inserted about 6 mm. apart; sheaths strongly compressed, sharply carinate, dark chestnut-brown, 6-8 mm. wide at base, 4-6 cm. long, the margins entire, the carina ciliate above, entire below: blades linear, 3-5 mm. wide, 5-8 cm. long beyond the sheath, obtuse or rounded, silvery-green, finely many-nerved, densely ciliate

with dark brown hairs; scapes strongly flattened and 2-edged, somewhat twisted, 25-45 cm. tall, sheathed at base with a nearly bladeless leaf, entire below, densely ciliate above; heads subglobose, 9-12 mm. long; bracts all obtuse or rounded, not carinate, reddish-brown, the dorsal area none or indistinct, the lowest 2 mm. long and ovate-lanceolate, the inner progressively larger and as much as 6 mm. long and 4 mm. wide, the outermost 6-8 pairs sterile and decussate, forming 4 vertical rows of 3-4 bracts each, the upper bracts spiral and fertile; lateral sepals 7 mm. long, narrowly oblong, acute, nearly equilateral, the margins subhyaline, the keel minutely fimbriate on the distal half; corolla and stamens not seen; capsule obovoid, loculicidal, 5 mm. long.

Type, *Tate 427*, collected on the summit of Mount Roraima,³ British Guiana, 26 Nov. 1927, and deposited in the herbarium of the New York Botanical Garden. In its strongly caulescent habit it is reminiscent of *X. witsenioides* Oliver, from which it differs in its ciliate leaves and scapes and decussate bracts. Its affinities seem to be rather with *X. spectabilis* Mart. and its relatives, constituting a small group on the campos of southern Brazil. These also have ciliate leaves and sterile lower bracts, but are regularly much larger in all dimensions and have spirally imbricate bracts throughout.

Xyris submontana Gleason, n. sp. Section NEMATOPUS: cespitose; leaves distichous, the sheaths sharply carinate, 1-2 cm. long, the blades narrowly linear, 7-13 cm. long, 2-3 mm. wide, acuminate to a subulate tip, glabrous; scapes 4-6 dm. tall, very slender, slightly flattened, the basal sheath about 10 cm. long, nearly bladeless; heads subglobose, 8-10 mm. high; outer bracts broadly ovate, 4 mm. long, the distal margin scarious and lacerate; principal bracts with a firm, brown, broadly cuneate-obovate body 5-6 mm. long, terminated distally by a scarious lacerate margin 2-3 mm. long, the dorsal area not differentiated; lateral sepals obtuse, broadly spatulate or narrowly obovate, 3.5-4 mm. long, 1.2 mm. wide, the thin membranous margins nearly equilateral, the keel finely but conspicuously and rather densely ciliate over nearly its whole length.

Type, *Tate 334*, collected in Philipp Swamp, Mount Roraima, British Guiana, alt. 5100-5200 ft., 11 Nov. 1927, and deposited

³ The small area on the summit of Mount Roraima is shared by Brazil, Venezuela, and British Guiana, and the dividing line between them has not been accurately located. All species mentioned in this article from the summit and slopes of the mountain have been credited to British Guiana as a matter of convenience.

in the herbarium of the New York Botanical Garden. Its relation seems to be with *X. concinna* N. E. Brown, another Roraima species, which it resembles in its broadly scarious-margined bracts. It differs, however, in its general size, the leaves being nearly twice as long and wide and the scape three times as tall as in *X. concinna*, and in the shape of its lateral sepals, those of *X. concinna* being 5-6 mm. long and less than 1 mm. wide.

Syngonanthus biformis Gleason, new comb. (*Paepalanthus biformis* N. E. Brown.) This endemic species is undoubtedly a *Syngonanthus*, as already recognized by Ruhland. In this recent monograph he united it with *S. simplex* (Miq.) Ruhl., from which it is abundantly distinct. At the edge of water, Frechal, extreme northern Brazil: no. 21; also from above 5000 ft. on Mount Roraima: without number.

Syngonanthus glandulosus Gleason, n. sp. Leaves linear, spreading or recurved, about 10 mm. long, 1.5 mm. wide, 7-nerved, finely puberulent beneath, conspicuously pubescent with appressed hairs above, from a densely lanate stem; peduncles 7-11 cm. long, glandular-pubescent with hairs 0.4-0.5 mm. long, roundly 3-costate, lightly twisted; sheaths twisted, about 1 cm. long, thinly hirtellous, terminating in an ovate-lanceolate acuminate lamina 5 mm. long, the sides meeting in a rounded sinus; heads hemispheric, about 7 mm. in diameter; outer bracts imbricate, the inner progressively longer, scarious, glabrous, lanceolate to elliptic oblong, sharply acute, as much as 3 mm. long by 1.1 mm. wide; subtending bracts none; receptacle villous; staminate flowers: pedicels 0.6 mm. long; sepals rhombic-elliptic, 1.8 mm. long, 0.7 mm. wide, more or less naviculate, sharply acute or acuminate, not falcate, glabrous, the posterior a trifle shorter and narrower; petals united into an obconic tube 0.5 mm. long with 3 very short lobes; pistillate flowers: pedicels 0.2 mm. long; sepals ovate-lanceolate, 2.2 mm. long, 0.6 mm. wide, acuminate, hyaline, glabrous; petals narrowly cuneate-obovate, separate and densely pubescent below, connate about the middle, the lobes involute and tangled; pistil just equaling the corolla, the ovary 0.6 mm. long, the terete style, filiform simple stigmas, and filiform capitate appendages each 0.3 mm. long.

Type, *Tate 345*, collected at Philipp Swamp, in the Roraima district of British Guiana, alt. 5100-5200 ft., 11 Nov. 1927, and deposited in the herbarium of the New York Botanical Garden. The plant consists of a number of short erect stems which are

densely leafy and send out numerous peduncles from the upper axils. In general habit it resembles *S. simplex*, *gracilis*, and *bi-formis*, and differs from the first in its appendaged style, from the second in its narrow acute bracts, from the last in its symmetrical sepals, and from all three in the rounded sinuses of its peduncular sheaths.

PLEUROTHALLIS VAGINATA Schlechter. In humid forest on Mount Roraima at 6900 ft.: *no. 489*. This collection records an extension of the known range of the species from Costa Rica into South America.

Four undescribed species of orchids have been detected in the collection by Professor Ames and will be described by him elsewhere.

Chamaecrista bauhiniaefolia (Kunth) Gleason, new comb. (*Cassia bauhiniaefolia* Kunth) Small marsh near Limao, extreme northern Brazil: *no. 121*.

Chamaecrista Roraimae (Benth.) Gleason, new comb. (*Cassia Roraimae* Benth.) Along the Kukenaam river at Roraima ford: *no. 176*.

Aeschynomene laxa Gleason, n. sp. Suffrutescent, erect, freely branched, 5 dm. high or more; stems slender, terete, essentially glabrous, sparsely marked with minute purple spots bearing a single short central hair; stipules soon deciduous, linear-subulate, the terminal lobe 4–6 mm. long, the basal 1.5–3 mm. long; principal leaves 5–6 cm. long, erect, with 50–70 leaflets, the upper much smaller with fewer leaflets; leaflets obliquely elliptic-oblong, rounded and minutely apiculate at the summit, the midvein central, varying in size from 3 mm. at the base to 1.5 mm. long at the summit of the leaves, or only 1 mm. on the uppermost leaves; racemes axillary, about 5-flowered, elongating during anthesis to 6 cm., the rachis spotted like the stem; pedicels 3 mm. long, becoming 5–7 mm. in fruit; prophylla oblong-elliptic, 1.3 mm. long; calyx (including the hypanthium) 3.1–3.2 mm. long, its tube 1.2–1.3 mm., deeply bilabiate, the upper lip with 2 ovate rounded lobes 0.5 mm. long, the lower with 3 oblong-ovate lobes 0.6–0.7 mm. long; vexillum round-spatulate, 4 mm. long, dotted with purple; fruiting stipe slender, 7 mm. long; joints of the legume 2, rhombic-ovate, 3.5 mm. long, 3 mm. wide, with much thickened sutures, slightly convex above, broadly rounded below, the surface somewhat veiny and glabrous.

Type, *Tate 10*, collected on the edge of a swamp at Frechal, in northern Brazil, south of Mount Roraima, 6 Sep. 1927, and

deposited in the herbarium of the New York Botanical Garden. It is most closely related to *A. filosa* Mart., from which it differs in its smaller flowers, less deeply lobed calyx, purple-dotted vexillum, and narrower stipules.

Bowdichia parvifolia Gleason, n. sp. Tree, height not stated; branches finely brown-pubescent or subvelutinous; petioles 2–2.5 cm. long, thinly pubescent; rhachis of the once-pinnate leaves more densely pubescent; leaflets 5–11, sessile, firm or coriaceous, narrowly oblong-lanceolate, 12–18 mm. long, 3–5 mm. wide, obtuse, slightly revolute, cuneate at base, minutely pubescent and reticulately veined above, densely pubescent, especially on the midvein, beneath; panicle ample, terminal, consisting of several racemes 5–10 cm. long, the lowest subtended by foliage leaves; peduncle 3–5 cm. long, with the rhachis minutely puberulent, bearing 5–10 flowers on pedicels 3–5 mm. long with a pair of minute bractlets near the middle; hypanthium campanulate, fleshy, 3.6 mm. long; calyx-tube gradually widened upward, subfleshy, 3.6–4 mm. long, purple distally; calyx-lobes erect, broadly triangular, 1.5 mm. long by nearly twice as wide, densely white-ciliate, sparsely pubescent externally, separated by narrow acute sinuses; standard broadly flabellate-cuneate, the claw 3 mm. long, the blade 8 mm. long, 13 mm. wide, deeply emarginate, erose and crisped; wings with a claw 5 mm. long, the blade obovate, 10 mm. long, 7 mm. wide, rounded and erose distally; keel petals separate, narrowly oblanceolate, 10 mm. long, the claw gradually widened into a blade 3 mm. wide; stamens 10, separate, filaments subulate, ultimately somewhat exceeding the sepals and 6 mm. long; anthers versatile, broadly elliptic, 0.8 mm. long; ovary on a glabrous stipe 2.7 mm. long, straight, many-seeded, 4 mm. long, thinly villous; style slender, abruptly incurved to the capitate stigma.

Type, collected by *Tate* without number, on the savanna at Frechal, south of Mt. Roraima, northern Brazil, 30 Sep. 1927, and deposited in the herbarium of the New York Botanical Garden. Of the true *Bowdichias* with stipitate ovary only two species have hitherto been described. The common *B. virgilioides* has leaves three times as long and five times as wide with an almost or quite glabrous ovary, and *B. nitida* Spruce has similarly large leaves and is glabrous throughout, except for the ovary.

QUALEA SCHOMBURGKIANA Warm. Our specimen agrees in all essential features with Schomburgk's original specimen and with Warming's description, but has larger flowers, the petal

being 5 cm. long and 5.5 cm. wide. A tree on the riverside at Arabupu, Mount Roraima, alt. 4200 feet: *no. 206*.

Polygala microspora Blake, n. sp. Tiny glabrous annual, branched above; leaves alternate, linear, 7 mm. long or less; racemes dense, acute, 4-7 mm. long, 2-3 mm. thick, scarcely comose; flowers white; wings oval, 1.5-1.7 mm. long; keel with small, slightly lobed crest; capsule oval, 1.2 mm. long; seeds pyriform, glabrous, black, 0.5 mm. long, minutely favose; aril reduced to a minute knob.

Plant slender, 3-5 cm. high, leafy, the somewhat spreading branches up to 2.5 cm. long; leaves acutely callous-pointed, fleshy, 4-7 mm. long, 0.3-0.5 mm. wide; racemes short-peduncled, conic-cylindric; bracts ovate, short-acuminate, 0.7 mm. long, glabrous, with greenish center and pale margin, deciduous (?); pedicels spreading, about 0.3 mm. long; upper sepal oval, obtuse, 0.8-1 mm. long, whitish with greenish biglandular thickening at base, obscurely erose above; lower sepals similar, oval-ovate, 0.5 mm. long; wings scarcely clawed, broadly rounded, sometimes obscurely erose above, 3-nerved, 0.9-1.2 mm. wide; keel 1.2 mm. long, the crest on each side of a broadly triangular sometimes bifid lobe; upper petals obovate-oblong, truncate-rounded, about 2-veined, 1.4 mm. long; anthers 6, longer than the glabrous free portion of the filaments; style short, thick, scarcely longer than the stigmata; upper stigma excavate, with a short nearly sessile crest; capsule rounded, emarginate, 0.9 mm. wide; seed pointed at base, rounded and minutely umbonate at apex.

Brazil: edge of marsh, Frechal, near Mt. Roraima, 6 Sept. 1927, *G. H. H. Tate 15* (type in herb. N. Y. Bot. Gard.; photog. and fragm., U. S. Nat. Herb.).

A species of the *Tenuis* group of the subgenus *ORTHOPOLYGALA*, related to *P. subtilis* H. B. K. and *P. gracillima* S. Wats., but at once distinguished by its pyriform seed. From description, it was first thought that the specimens might be referable to *P. Spruceana* A. W. Bennett. Examination of the type (*Spruce 3734*) of that species, made available through the kindness of Dr. A. W. Hill, has shown that while the two species are similar in appearance, the seed of *P. Spruceana* is nearly oblong, 1 mm. long, and provided with a two-lobed aril 0.8 mm. long.—S. F. BLAKE.

Chaetocarpus stipularis Gleason, n. sp. Low tree; stems terete, minutely appressed pubescent with ferruginous hairs when young, glabrous in age, the internodes 2-4 cm. long;

stipules subcoriaceous, erect, inequilaterally ovate, 10 mm. long, 5 mm. wide, acute, glabrous, 2-3 nerved; petioles narrowly winged, 3 mm. long, sparsely pubescent, soon becoming glabrous; leaf-blades coriaceous, shining, ovate-lanceolate, 6-8 cm. long, 3-4.5 cm. wide, acuminate to an obtuse apex, entire, obtuse at base, glabrous, the lateral nerves 6-8 on each side, the veinlets reticulate, scarcely elevated; pistillate flowers fascicled in the upper axils, sessile or with pedicels 1-3 mm. long; pedicels and calyx minutely but densely pubescent; sepals imbricate, broadly ovate, ciliate; petals none; fruiting pedicels 5-7 mm. long, nearly smooth; capsules woody, 1 cm. long, subspherical, densely echinate, the echinae obtuse, terminated by a short, deciduous hair; valves bifid to the middle; seeds short-stipitate, ovoid, 6 mm. long, black and shining, somewhat flattened on the sides, rounded on the back, tipped with a large, 2-lobed, red caruncle.

Type, *Tate 194*, collected on the river-side at Arabupu, Mt. Roraima, alt. 4200 ft., 1 Jan. 1928, and deposited in the herbarium of the New York Botanical Garden. *C. stipularis* differs from *C. Schomburgkianus* Pax & K. Hoffm., the only species hitherto known from the region, in its shorter, more shining leaves on much shorter petioles, its much larger stipules of entirely different shape, and in some details of the fruit and seeds. There are still one or two other undescribed species in British Guiana.

CYRILLA BREVIFOLIA N. E. Brown. Summit of Mount Roraima: *no. 387a, 401*; on savannas at Arabupu, slopes of Mount Roraima, alt. 4200 feet: *no. 287*. The species was originally collected on, and supposed to be endemic to, the summit of the mountain. Our specimen from the lower altitudes has much larger leaves, up to 35 mm. in length, with the lateral veins more evident.

WEINMANNIA LAXIRAMEA Killip & Smith. Summit of Mount Roraima: *no. 395*.

WEINMANNIA VENEZUELENSIS Killip & Smith. Summit of Mount Roraima: *no. 383*.

MELOCHIA PARVIFOLIA HBK. A form with unusually small leaves, on hardpan soil at Limao, extreme northern Brazil: *no. 97*.

Ouratea Tatei Gleason, n. sp. Arborescent, glabrous throughout; branches brown, the bark soon exfoliating; petiole stout, 1 cm. long, channeled above; leaf-blades coriaceous, opaque,

oblong, 13–16 cm. long, 27–57 mm. wide, broadly acute at base, entire, acuminate to a subacute apex, the lateral veins obscure, strongly curved-ascending; panicle terminal, freely branched, 20 cm. long; pedicels 3–6 mm. long, slender; buds ovoid, acute, 6 mm. long; sepals ovate-lanceolate, acute, the outer two with very narrow scarious margins, the inner two broadly scarious on each side and the intermediate one scarious on one side; petals yellow, herbaceous, broadly spatulate-rotund from a cuneate base or claw, 9 mm. long, 7.5 mm. wide; anthers nearly sessile, subulate, straight, 6 mm. long; gynophore about equaling the ovaries; carpels 5, 1 mm. long, ovoid; style stout, 6.5 mm. long, gradually tapering from the base to the punctiform stigma.

Type, *Tate 220*, collected in humid, deeply shaded ground in the Weitipu forest, Arabupu, on the slopes of Mount Roraima, British Guiana, alt. 4200 ft., 1 Jan. 1928, and deposited in the herbarium of the New York Botanical Garden. The same species is also represented in the Kew herbarium by an unnumbered collection of Im Thurn from the same locality. It is most closely related to *Ouratea rigida* Engl. from the Rupununi region south of Roraima.

Hypericum roraimense Gleason, n. sp. Section BRATHYS, subsection EUBRATHYS; fruticose; stems freely branched, about 2 dm. long, 4-angled above, the internodes 1–1.5 mm. long; leaves crowded and concealing the stem, firm or subcoriaceous, spreading or ascending, sessile, flat, slightly carinate toward the base, narrowly oblong-lanceolate, 7–10 mm. long by a fifth as wide, 1-nerved with two pairs of faint ascending lateral nerves, acute, entire; flowers solitary, terminal, the pedicels 1.5 mm. long and much exceeded by the upper leaves; sepals lanceolate, acute, erect, firm, two 5.7 mm., two 5.1 mm., one 4.7 mm. long by a third as wide, 3-nerved; petals persistent, yellow, obliquely obovate-oblong, 9 mm. long, 3 mm. wide, several-nerved; stamens about 25, separate to the base, the filaments 4–5 mm. long; ovary 1 celled with 2 or 3 placentae, 1.7 mm. long; styles 2 or 3, separate to the base, erect, subulate, 4.6 mm. long.

Type, *Tate 412*, collected on the summit of Mt. Roraima, alt. 8650 ft., 27 Nov. 1927, and deposited in the herbarium of the New York Botanical Garden. It is obviously closely related to the Andean species, which it resembles in habit and in general structure. Of the latter, but three species agree in the possession of flat narrow leaves and 3 styles conspicuously longer

than the ovary. *H. Jussiaei* and *H. thymifolium* have shorter petals, styles, and filaments and about twice as many stamens, while the third, *H. Phellos* Gleason, has much larger petals, longer styles, and about 100 stamens. Various species of the genus are known from the Venezuelan Andes, but *H. roraimense* is the first species reported from the Guianas.

Tibouchina pseudomollis Gleason, n. sp. Stem densely hirsute with pale brown, ascending, simple hairs 1-1.5 mm. long, less densely so above, the internodes 3-6 cm. long; petioles hirsute like the stem, 3-5 mm. long; leaf-blades firm, ovate-lanceolate, the largest 41 mm. long and 19 mm. wide, the upper somewhat reduced, acuminate, minutely serrulate, abruptly acute at base, 5-nerved, upper surface densely hirsute with ascending simple hairs 2-3 mm. long from an adnate base, lower surface hirsute with whitish hairs 1-3 mm. long from a simple base; inflorescence a freely branched panicle, the nodes subtended by bracteal leaves 10-15 mm. long; flowers 5-merous; hypanthium tubular-campanulate, 10-ribbed, 5 mm. long to the torus, villous with ascending simple hairs 2-2.7 mm. long from papillose bases; calyx-tube prolonged 0.4 mm., somewhat flaring, the acute sinuses subtended by straight, simple, reflexed setae nearly 3 mm. long; sepals with a broadly deltoid membranous base 2.4 mm. wide and 1.3 mm. long, tipped by a stoutly subulate apex 2.3 mm. long, ciliate throughout, the prominent midrib hirsute; petals broadly obovate, pink, 8 mm. long, 7 mm. wide, finely ciliate with glandular hairs; stamens essentially isomorphic and equal; filaments straight, subterete, glabrous, 5-6.7 mm. long; anthers stoutly subulate, 4.4 or 5 mm. long; connective prolonged 0.7 or 1.3 mm. to the apex of the filament, with a small dorsal basal protuberance and two deflexed basal ventral lobes 0.4 mm. long; ovary half inferior, 5-celled with intruding placentae, short-hirsute on the free summit and tipped with a crown of erect terminal cilia; style glabrous, straight, 10.5 mm. long, narrowed slightly below the capitate stigma.

Type, *Tate 275*, collected on sandstone boulders at Philipp Camp, Mt. Roraima, alt. 5200-6000 ft., 7 Nov. 1927, and deposited in the herbarium of the New York Botanical Garden. It is a member of the section *Diotanthera*, with the general habit of the Andean *T. mollis*.

Siphanthera cordifolia (Benth.) Gleason, new comb. (*Meisneria cordifolia* Benth., *Siphanthera microlicioides* Cogn.) Philipp Swamp, on the slopes of Mount Roraima, alt. 5100-5200 feet: *no. 341*.

An unidentified sterile specimen of a Vacciniaceous shrub was collected on the upper slopes of the mountain: *no.* 284. This is identical with *Schomburgk* 566, from about the same locality, which is also sterile.

BEJARIA (BEFARIA) IMTHURNII N. E. Brown. Summit of Mount Roraima: *no.* 407. Three small branches of this species, two in flower and one with young fruits, represent Im Thurn's original collection in the Kew herbarium. Oliver did not assign them a specific name, but did recognize that two forms were included, as shown by his published report and by his pencilled note on the sheet. Whether by accident or design, one sheet bears two twigs of one form and a second sheet a single stem of the other, which was obviously mounted there after Oliver's report was printed. Brown, in drawing up his specific description, had the additional advantage of twelve twigs collected by Quelch and McConnell. Of the total of fifteen twigs, the two collected by Im Thurn and labeled by Brown are logically the type. Brown also saw the two forms and drew up his description to include both. Since the differences between them lie in three sets of characters and are perfectly constant, the two may well be separated as distinct species. The distinctive characters of *B. Imthurnii* are: stem and pedicels densely pubescent to nearly glabrous, with slender, tapering, non-glandular hairs; leaves ciliate to entire, the cilia when present of slender simple bristles; midvein often ciliate toward the base; sepals erose-denticulate to fimbriate. In the second form, described below, the characteristic features are the callous black glands along the leaf-margin, the glandular hairs on the stem and midvein, and the entire sepals.

Bejaria Tatei Gleason, n. sp. A low, freely branched shrub; stem and pedicels densely pubescent with spreading, dark-brown, glandular hairs 0.6–0.9 mm. long, the glands frequently deciduous on the older parts; internodes 1–4 mm. long; leaves crowded toward the end of the branches, their blades coriaceous, light green above, greenish white beneath, elliptic or oblong, 15–25 mm. long by half as wide, or the uppermost somewhat smaller, subacute, slightly revolute, tapering at base into a margined petiole 1–3 mm. long, the margin densely (5–7 per mm.) scabrid with conic or truncate-conic black callous glands 0.2–0.3 mm. long and the apex of the blade transformed into a similar gland; midvein, especially along its basal

half, with stalked glands 0.4–0.8 mm. long; inflorescence a crowded abbreviated terminal raceme; pedicels glandular like the stem, 5–15 mm. long; hypanthium broadly campanulate to hemispheric, 1.3–1.6 mm. long, red, sometimes glandular-pubescent; petals oblong, retuse, about 2 cm. long; sepals broadly triangular-ovate, subacute, glabrous, nearly or quite entire.

Type, *Tate 408*, collected on the summit of Mt. Roraima, alt. 8650 ft., 24 Nov. 1927, and deposited in the herbarium of the New York Botanical Garden. Other material in the Kew herbarium is *Im Thurn* without number, *Quelch and McConnell 94* (in part) and *646* (in part).

Calolisianthus Imthurnianus (Oliver) Gleason, new comb. (*Lisianthus Imthurnianus* Oliver) Summit of Mount Roraima: no. 442.

Symbolanthus Quelchii (N. E. Brown) Gleason, new comb. (*Lisianthus Quelchii* N. E. Brown) Summit of Mount Roraima: no. 397.

CHELONANTHUS sp., the same as *Ule 8448* from the Rio Branco, alt. 3000–4000 ft., which has been identified as *C. Schomburgkii* (Griseb.) Gilg. It does not match the type of that species, *Schomburgk 298*, which has the broad connate leaves of *C. chelonoides*. The specimen consists of a fruiting plant 6 dm. high, and an apparently depauperate flowering plant 4 dm. high, bearing a corolla only 25 mm. long. The flowers of the *Ule* plant are 42 mm. long. It probably represents an undescribed species, but no name has been assigned because of the lack of suitable flowers for examination. Lower slopes of Mount Roraima: no. 179.

MANDEVILLA sp. Slopes of Mount Roraima at Arabupu, alt. 4200 feet: no. 228. This plant is the same as *Ule 8450* in the Kew herbarium, which has been named *M. Schomburgkii* K. Schum. This name has apparently not been published. Our material is insufficient to justify describing it as the type of a new species.

HYDROLEA MULTIFLORA Mart. In marshes at Frechal and Limao, extreme northern Brazil: no. 14, 76. This obscure species has been very poorly represented in herbaria. The new material permits me to offer the following emended description of its floral characters.

Sepals 5, separate, oblong-lanceolate, 3.2 mm. long, enlarging during anthesis to 5.5 mm., acute, 1-nerved, obscurely reticulate, glabrous (no. 14) or thinly glandular-puberulent (no. 76); corolla campanulate, the tube stout, expanding from 0.6 to 1.2 mm. in length, its 5 lobes equal, enlarging from 1.9 to 3.5 mm. long; stamens 5, equal, inserted between the corolla-lobes; filaments 0.2 mm. wide at base, eventually 2.6 mm. long; anthers dithecous, versatile, the two halves almost separate, curled, longitudinally dehiscent; ovary stoutly ellipsoid, 2 mm. long, the axial placentae thick and protruding, with numerous ovules; styles 2, 2 mm. long, slender, diverging at base, inarched at the summit; stigmas capitate; fruit a many-seeded capsule.

LANTANA sp. Riverside at Arabupu, slopes of Mount Roraima, alt. 4200 feet: no. 195. This is the same as *Jenman* 6339 from the Rupununi savannas, erroneously labeled *L. mixta* L. in the Kew herbarium. It may well be an undescribed species, but no name has been assigned to it because of the confusion affecting many species of the genus.

CACONAPEA AURICULATA (Rob.) Pennell. Close to *Herpestis gracilis* Benth., from Brazil, which seems to differ in outer sepals 'oblong,' rather than triangular-acuminate, and plant wholly glabrous (not even puberulent), but which may show real contrasts when we can see authentic specimens of it. In a marsh at Limao, extreme northern Brazil: no. 120.—F. W. PENNELL.

Caconapea verticillata Pennell & Gleason, n. sp. Stem erect or ascending from a creeping base, 5–8 cm. long, 4-angled, below glabrous, above with sessile yellowish glands; leaves apparently in whorls of 6, actually opposite, each cleft nearly or quite to the base into 3 linear, distally dentate, glandular-dotted segments 3–5 mm. long; pedicels 1 or 2 in an axil, scarcely evident; bractlets subulate, 1 mm. long; sepals glabrous and glandular-dotted, the outermost 3 mm. long, elliptic-lanceolate, two median narrower and one-sided, these three green, obtuse or mucronulate, minutely ciliate, two innermost lanceolate-attenuate, widely hyaline margined, 2–2.5 mm. long; corolla 2.5 mm. long, glabrous throughout, probably white, the posterior lobes united for part of their length, the three anterior lobes spreading; filaments glabrous, the posterior pair shorter; anthers uniform; style glabrous; stigmas 2, spreading; capsule 2–2.2 mm. long, ellipsoid-oblong, glabrous, dehiscent nearly loculicidally; placentae narrow, thin, median to the septum; seeds 0.2–0.3 mm. long, cylindric, brown, not evidently reticulate.

Type, *Tate 72*, collected on mud where water is receding at Limao, extreme northern Brazil south of Mount Roraima, 21 Sep. 1927, and deposited in the herbarium of the New York Botanical Garden; isotype at the Academy of Natural Sciences of Philadelphia. It differs from other species by its cleft leaves, and, at least from those of Columbia, also by loss of reticulations on the seed-coat.—F. W. PENNELL.

Stomoisia spicata (Sylvén) Gleason,⁴ new comb. (*Utricularia spicata* Sylvén). This species was described in 1908 from material collected by Malme in 1903 at Cuyabá, Matto Grosso, and does not seem to have been reported from any other locality. It is very distinct from all other American species of *Stomoisia* by the manner in which its calyx-lobes become accrescent after flowering, enclosing and much exceeding the capsule like large valves, their edges appressed to each other so that the effect to the eye is like that of a winged fruit. Tate's locality is also in Brazil, but more than a thousand miles north of Cuyabá, and at first sight such a distance might seem unreasonable. But the intervening country is little explored and is mostly covered with a dense tropical forest, a country poorly adapted to the growth of this savanna-loving plant. In water at Frechal, extreme northern Brazil: *no. 19*.—J. H. B.

Calpidisca calycifida (Benj.) Gleason, new comb. (*Utricularia calycifida* Benj.) Philipp Swamp, Mount Roraima, alt. 5100–5200 feet: *no. 342*.

Calpidisca Humboldtii (Schomb.) Gleason, new comb. (*Utricularia Humboldtii* Schomb.) Philipp Swamp, Mount Roraima, alt. 5100–5200. *no. 316*. When Robert Schomburgk first visited the upper slopes of Roraima, in 1838, he found there a beautiful dark blue flower, called by the natives 'Roraima iperua,' the 'Flower of Roraima.' This he described in 1840 under the above name. It has the largest and most conspicuous flowers of any Lentibulariaceous plant, and well deserves the praise that has been showered upon it. Schomburgk found it in only one place, but further exploration has revealed a somewhat wider distribution. Two marked forms are known, which

⁴ The segregation of the polymorphic genus *Utricularia* is due primarily to the careful studies of Dr. Barnhart, who identified this and the following five other species of the family. At his own request, the six new combinations made here have been credited as printed.

may eventually prove to be distinct species; the dark-flowered terrestrial form, apparently confined to the higher slopes of Roraima, above 1500 meters, and a paler-flowered form growing in water in the leaf-bases of the bromeliad *Brocchinia cordylinoides* on Kaieteur Savanna, at about 300 meters, where it was discovered by Im Thurn in 1884. No morphological differences between the two forms, however, have yet been noted. The *Brocchinia* grows in both places, also showing two strikingly different forms, and it is said that the dark-flowered Roraima *Calpidisca* is sometimes, although rarely, found associated with the *Brocchinia* leaf-bases. Tate did not approach Roraima over the usual route, by Kaieteur, and his specimens are of the Roraima form.—J. H. B.

Calpidisca roraimensis Gleason, new comb. (*Utricularia roraimensis* N. E. Brown) Summit of Mount Roraima: no. 386.

Orchyllium Campbellianum (Oliver) Gleason, new comb. (*Utricularia Campbelliana* Oliver) Rondon Camp, Mount Roraima, alt. 6900 feet: no. 514a. Although not named and described until 1886, the description was based upon plants collected on the upper slopes of Mount Roraima by Schomburgk many years earlier. The collections by Im Thurn in 1884, by McConnell and Quelch in 1894, and by Tate in 1927 were all from the upper slopes. This and *O. Quelchii* appear clearly distinct, but they are very closely related; both have crimson corollas, a rare character in the genus *Orchyllium*.—J. H. B.

Orchyllium Quelchii Gleason, new comb. (*Utricularia Quelchii* N. E. Brown) Summit of Mount Roraima: no. 375.

Cephaelis Tatei Standley, sp. nov. Omnino glabra, ramulis gracilibus, obtuse tetragonis, internodiis 2–4.5 cm. longis; stipulae 4–5 mm. longae, persistentes, erectae, fere ad basin bifidae, lobis ovalibus, apice rotundatis; folia opposita, petiolo gracili, 8–13 mm. longo; lamina oblonga vel anguste oblonga, 11–17 m. longa, 2.5–5 cm. lata, longe sensimque acuminata, basi acuta, subcoriacea, supra viridis, nervis manifestis sed non elevatis, subtus pallidior, olivacea, costa gracili, elevata, nervis lateralibus utroque latere c. 13, gracillimis, prominulis, angulo lato adscendentibus, arcuatis, marginem fere attingentibus, nervulis manifestis, reticulatis; inflorescentia terminalis, 5–6.5 cm. longe pedunculata, capitato-umbellata, capitibus 4–5, densis, paucifloris, pedunculis 1.5–2.5 cm. longis; bracteae exteriores late ovatae vel ellipticae, acutae vel ob-

tusae, 1.5–2 cm. longae, 1–1.5 cm. latae, interioribus brevioribus; flores sessiles; calyx persistens, truncatus, 0.8 mm. longus; fructus ovali-globosus, 6–7 mm. longus, obtuse costatus.

British Guiana: Arabupu, slopes of Mount Roraima, alt. 1260 m., Jan. 1, 1928, *G.H.H. Tate 262* (Herb. N. Y. Gard., type).

Although several apparently related species of *Cephaelis* have been described from Roraima, none of them agrees in all its respects with the present plant.—P. C. STANDLEY.

Viburnum roraimense Killip & Smith, n. sp. Tree, glabrous throughout, the branches subangular; petioles 8–15 mm. long; leaf-blades ovate, 8–12 cm. long, caudate-acuminate (tip 1–2 cm. long), rounded or subacute at base, subentire, conspicuously reticulate-veined, the nerves about 6 to a side, arcuate-ascending; peduncles 4–8 cm. long, usually slightly curved; bracts narrowly elliptic-spatulate, 3–4 cm. long, 5 mm. wide, conspicuously reticulate-veined, deciduous; corymbs 7- or 8-rayed, 5–8 cm. wide, 2- or 3-times branched, bracteolate, the bractlets about 1 mm. long, soon deciduous; calyx-tube 1–2 mm. long, glabrous, very sparsely glandular-punctate, the lobes ovate, rounded, 0.6–0.7 mm. long, faintly ciliate; ovary furrowed; fruit (immature) ovoid, greenish.

Type, *Tate 500*, collected 4 Dec. 1927 on Mount Roraima, British Guiana, alt. 2100 m., and deposited in the herbarium of the New York Botanical Garden. The species is also represented by Jenman's *220*, collected in the same locality.

BACCHARIS sp. Savanna at Arabupu, slopes of Mount Roraima, alt. 4200 feet: *no. 273*. This is the same as *Appun 1165* from the same locality.

2. ADDITIONS TO THE KNOWN FLORA OF RORAIMA

In the only enumeration of the montane flora of Roraima, Brown listed 239 species of seed-plants from elevations exceeding 5000 feet. No summary has been made of the number of species collected by Ule. The Tate collection includes apparently 157 species, of which 134 have been fully identified, and from them 50 species of seed-plants may now be added to the list, bringing the total to 289 species, and it would doubtless be well over 300 if the results of the Ule explorations were also incorporated.

There is no distinct vegetation-line on the mountain at 5000 feet, this level being chosen arbitrarily by Brown, probably

because it is higher than any other mountains in the Guianas, except those of the immediate neighborhood of Roraima. Considering the general luxuriance of tropical vegetation, we may well be surprised at the small number of species known, which will probably be doubled after thorough botanical exploration. The mountain needs especially exploration at other seasons of the year; Brown noted that all visits to the higher altitudes had been made late in the year, and both Ule and Tate followed the usual precedent.

Among the 50 species to be added, a part includes species of wider distribution, frequently extending far from the Roraima region. These may have been known already from Roraima, but only from the lower levels, and are now reported from the upper levels for the first time. The second group comprises endemic species only, some of which have been previously known from the lower levels and others of which are here described for the first time. Not every specimen listed was collected first by Tate; several in both groups were detected by Ule and have been described from his material.

Group 1. Non-endemics

- | | |
|----------------------------------|---------------------------------------|
| PANICUM CARANNASENSE Mez | CLUSIA ROSEA Jacq. |
| PANICUM CYANESCENS Nees | PTEROLEPIS GLOMERATA (Rottb.) |
| PASPALUM CONTRACTUM Pilger | Miq. |
| THRASYA PETROSA (Trin.) Chase | RAPANEA GUYANENSIS Aubl. |
| TRACHYPOGON PLUMOSUS (H. & B.) | BLEPHARODON STEUDELIANUS (Miq.) |
| Nees | Pulle |
| CAREX PURDIEI Boott | NEPHRADENIA ACEROSA Dcne. |
| XYRIS JUPICAI L. C. Rich. | BUCHNERA ROSEA HBK. |
| ERIOCAULON HUMBOLDTII Kunth | CALPIDISCA CALYCIFIDA (Benj.) Gleason |
| ELLEANTHUS AUREUS Reichb. f. | SETISCAPELLA SUBULATA (L.) Barnh. |
| EPIDENDRUM REPENS Cogn. | STOMOISIA JUNCEA (Vahl) Barnh. |
| HABENARIA DECIPIENS Lindl. | EMMEORHIZA UMBELLATA (Spr.) K. |
| MALAXIS HASTILABIA (Reichb. f.) | Schum. |
| Kuntze | ACHYROCLINE SATUREIODES (Lam.) |
| PLEUROTHALLIS VAGINATA Schlecht. | DC. |
| PEPEROMIA BASELLAEFOLIA HBK. | EUPATORIUM INULAEFOLIUM HBK. |
| WEINMANNIA VENEZUELENSIS Killip | EUPATORIUM LAEVIGATUM Lam. |
| & Smith | MIKANIA MICRANTHA HBK. |
| POLYGALA ADENOPHORA DC. | |
| POLYGALA FENDLERI Chod. | |

Group 2. Endemics

XYRIS DECUSSATA Gleason	MAHUREA EXSTIPULATA Benth.
XYRIS RORAIMAE Malme	PASSIFLORA SCLEROPHYLLA Harms
XYRIS SUBMONTANA Gleason	GRAFFENRIEDA OBLIQUA Triana
SYNGONANTHUS BIFORMIS (Brown) Gleason	TIBOUCHINA PSEUDOMOLLIS Gleason
SYNGONANTHUS GLANDULOSUS Gleason	BEJARIA TATEI Gleason
DROSERA MONTANA RORAIMAE (Kl.) Diels	BLEPHARODON ULEI Schlecht.
WEINMANNIA LAXIRAMEA Killip & Smith	PALICOUREA OBTUSATA Krause
POECILANDRA RETUSA Tul.	SIPANEA GALIOIDES Wernham
HYPERICUM RORAIMENSE Gleason	VIBURNUM RORAIMENSE Killip & Smith
	CALEA TERNIFOLIA Oliver

This brings the total number of endemic species to 139, or slightly less than half. This proportion will be further decreased by more extensive exploration of the upper slopes of the mountain. Endemism is most pronounced on the summit. Excluding the Ule collections, 76 species of seed-plants are now known from this high plateau, and of these no fewer than 68, or nearly 90 per cent, are endemic.

A morphological study of some Phalarideae, with special reference to classification

WILLIAM E. RIECKEN

(WITH PLATES 20, 21 AND FOUR TEXT FIGURES)

Classifications of the Gramineae have been made at various times, some for purely economic reasons, others solely with the aim of describing them. The different classifications invariably make exceptions for certain genera or groups of genera because the characters selected as a basis for classification do not clearly differentiate them. Thus, one finds certain genera having some characteristics which would place them with one group while other characteristics obviously place them with another group.

Though considerable work has been done on some grasses, especially those of economic importance such as our cereals, yet there are certain species or genera on which little detailed morphological work has been done with the view of aiding in the determination of their proper position in the classification. Some interesting relationships in the structure and development of the floral parts of certain grasses of doubtful position are revealed from a morphological study of stained microtome sections.

The family Gramineae, including all true grasses, is in modern classifications divided into two great subfamilies: (1) the Poatae, exemplified by *Poa*, in which the spikelets are one- to many-flowered with reduced florets, if any, above the perfect ones, the rachilla articulating above the glumes, and the spikelets more or less laterally compressed; and (2) the Panicatae, with *Panicum* as an example, in which the spikelets have one perfect terminal floret with a sterile or staminate floret below, the rachilla articulating below the more or less dorsally compressed spikelets. The subfamilies are further subdivided into tribes each of which embraces a number of genera.

The basis of distinction between the two great subfamilies is especially unsatisfactory because of the use of such characters as the articulation of the rachilla above or below the glumes, the persistence of the glumes, and dorsal or lateral compression of the spikelets, which are, from the standpoint of natural relationship probably not very fundamental. Due to this artificial

characterization of these groups, genera have frequently been changed from one tribe to another or grouped together into the same tribe when there was no relation between them to warrant such grouping. There are yet some tribes which do not fit well in the subfamily in which they are classified, indicating that there is doubt as to their real affinities. This doubt arises from the fact that part of the characteristics indicate that they belong to one group while others would place them with the other group. Such conditions can be remedied only by a better knowledge and use of morphological characters.

One of the groups of genera which presents such uncertain classification is the tribe Phalarideae. In the spikelets of the grasses of this tribe are found usually three florets, the uppermost one being perfect, the lower either staminate as in *Torresia*, or rudimentary as in *Phalaris* and *Anthoxanthum*. These rudimentary florets have been overlooked or ignored in most descriptions and the spikelet described as having empty lemmas. In practically all modern classifications the Phalarideae are placed in the subfamily Poatae, in spite of the fact that the spikelets of the grasses of this subfamily have the perfect floret below and the upper lemmas empty or subtending either staminate or rudimentary florets. Yet it has seemed proper to place this tribe in this subfamily because its genera appear to be more closely related to the species of this group from their other structural characters. They have the articulation of the rachilla above the glumes and the laterally compressed spikelets which are characters used to distinguish the tribes of this subfamily.

It is the purpose of this paper to present such evidence from a morphological study of several genera of this tribe as will help in determining its proper position.

HISTORICAL

The earlier classifications attempted before 1860 were very loose, in that they did not distinguish the truly one-flowered spikelets from those having but one functional flower, and since they were worked out before the doctrine of evolution had had a substantial influence upon classification, no attempt was made to show evolutionary relationships as is found in the classifications made since then. An example of such an attempt

is found in the classification of Sinclair (1869), in which he uses as the basis for his division the number of florets apparent in each spikelet, the number of stamens and styles in each floret and the number of valves (lemmas and paleas) of the 'corolla'. He found it necessary to make nine distinct groups and also numerous exceptions for certain genera.

More recent classifications take into consideration the evolutionary development of the plants and attempt to arrange the groups in the order of their relationship to one another. In most cases we find the Gramineae divided into thirteen tribes which are grouped into two large subfamilies.

Bentham and Hooker (1883), Hackel (1889, 1890), and Lamson-Scribner (1897) divide the Gramineae into two subfamilies, the Panicaceae and the Poaceae, on the basis of the articulation of the rachilla above or below the glumes, the prolongation of the rachilla beyond the florets, and the number of florets in the spikelet. Bentham and Hooker and Lamson-Scribner further emphasize the arrangement of the fertile and sterile florets, placing those tribes which have the uppermost florets perfect in the Panicaceae. The former make exceptions in the Panicaceae for *Isachne*, *Beckmannia*, and a few species of *Setaria*, and in Poaceae the genera *Crypsis*, *Cornucopiae*, and *Alopecurus* of the tribe Phalarideae and the genera *Fingerhuthia*, *Polypogon*, *Coleanthus* and *Nardus* are exceptions, while Lamson-Scribner places the Phalarideae in the Poaceae, but explains that the perfect flower is uppermost with four empty glumes below. Hackel uses the length of the internodes as an additional differential character and states specifically that of the four glumes in the Phalarideae the two inner ones rarely act as flowering glumes for staminate flowers. This does not provide for *Torresia*, which the writer finds regularly having the two staminate florets below. Hackel includes in the Phalarideae the genera *Ehrharta*, *Microlaena*, *Tetrarrhena*, *Phalaris*, *Anthoxanthum* and *Hierochloë*.

Baillon (1894) stresses the same characteristics as those just discussed, but instead of forming two large subfamilies, he divides the Gramineae into eleven tribes, one of which is Phalarideae, and in this tribe includes the same genera as given by Hackel.

Lamb (1912) develops in detail the scheme suggested by Bessey that the Bambuseae are the most primitive of the Gra-

mineae, and that from this tribe may be derived three main phylogenetic lines based on the position of the larger flowers in the spikelet. One line, the Festucean line, contains those grasses having the larger flower at the base of the spikelet. With this group he connects the Festuceae, Agrostideae, Aveneae, Hordeae and Chlorideae. In a second, the Phalaridean line, having the larger flowers at the top, he includes the Phalarideae, Oryzeae and Paniceae. The third group, the Andropogonean line, having the larger flowers at the top and the spikelets in pairs, includes the Andropogoneae and Maydeae.

The writer considers the order of development in the spikelet to be a better indication of phylogeny than is the relative size of flowers offered by Lamb, for the *larger* flowers are not always the *older*, an example of which we find in *Torresia odorata*.

The most extensive recent work which has been done on classification of the Grasses is that of Hitchcock (1914, 1920). In his publications he divides the Gramineae into two sub-families on the basis of the number of florets in the spikelet, the relative position of the reduced or imperfect florets, and the articulation of the rachilla above or below the glumes. He, too, finds that exception must be made in his classification for the Phalarideae, which are grouped with the Poatae, for, instead of having the reduced florets above the perfect ones, this tribe has the rudimentary florets below the perfect one.

It is obvious that the bases used in the classification of the Gramineae have not been altogether very satisfactory. It is desirable to have a basis which would include the different genera without the necessity of making exceptions.

The double aim of any system of classification is to group plants for convenience in treatment and at the same time to represent as nearly as possible their actual relationships. Modern practice attempts to arrange plants on the basis of the complexity of their floral structures, placing the more primitive first and the more highly developed last. In their evolution from a common origin, species tend to vary. Because of this tendency and because this development does not follow the same straight line in the different variations, it is possible to find that some plants which have become most highly developed in one group may exhibit evidences of being far in advance

of the most primitive of the next higher group (see Hitchcock, 1920, p.2). It thus becomes difficult to arrange them on any basis and at the same time show their genetic relationships. A morphological examination of the species may aid in determining these relationships and in giving us a truer basis for comparing them.

MATERIAL AND METHOD

For this study there were available four species: *Phalaris canariensis* L., *Phalaris arundinacea* L., *Anthoxanthum odoratum* L., and *Torresia odorata* (L.) Hitchc. of the tribe Phalarideae. The material for *Phalaris canariensis* and *Anthoxanthum odoratum* was given to me by Dr. Weatherwax, who brought seeds of both species from Georgia. *Phalaris arundinacea* is found growing wild in clumps near Bloomington, Indiana, and *Torresia odorata* was obtained from clumps growing wild near Winamac, Indiana.

Phalaris canariensis was grown in the greenhouse from the seed, and successive generations were grown from the seeds produced by the greenhouse plants. The plants grew and thrived under these conditions, producing an abundance of viable seeds which germinated well after a period of rest. Seeds planted in flats in the greenhouse in the fall grew well during the winter and in April flowered and bore fruit. An attempt to grow plants the following June from these seeds which matured in April resulted in failure, but some of the same packet of seeds germinated and grew readily when planted the following September in the greenhouse.

Clumps of *Phalaris arundinacea* which were observed showed that it propagates very easily by underground stems. An unsuccessful attempt was made to grow it in the greenhouse from seed. The panicles were observed to bloom, and after blooming the spikelets appeared to contain well developed seeds, each appearing well filled and plump. Their failure to germinate led to an examination of some of the spikelets, which when opened were found to contain but a small dried up pistil instead of a well developed seed; the lemma and palea enclosing this withered pistil gave the spikelet the appearance of having a well developed seed. The same condition was found when spikelets of three other seasons were examined, yet it was possible to

trace the development of the embryo sac as far as the megaspore stage. Further study needs to be made to determine whether viable seeds are formed. Clumps of plants with the underground stems that have been dug up and grown in the greenhouse during the winter and then carried outside during the summer have not formed any inflorescences but have sent out new shoots at many of the upper as well as the lower nodes. These nodes with shoots form roots which take hold of the soil and make separate plants.

All of the material was fixed in chromo-acetic acid or formol-acetic-alcohol, dehydrated slowly, and embedded in paraffin, from which the sections ten microns thick were cut. All sections were stained with the triple stain, anilin safranin, gentian violet, and orange G.

The contracted panicles of *Phalaris canariensis* are dense, ovoid, 1-1.5 inches long. The laterally compressed spikelets contain one perfect terminal floret and two lower lemmas, all of which are wholly enclosed by the two boat-shaped glumes (figs. 1, 2). In longitudinal sections of the spikelet are found evidences of the rudimentary floret in the axil of each of the lower lemmas, which are often referred to as the second and third glumes. Thus this species has a spikelet which is fundamentally three-flowered with the two lower florets rudimentary (figs. 3, 4).

In the development of the panicle, the uppermost spikelets are the first to mature. The significant thing, however, is the order of the development of the parts of the spikelets, which is found to be from the lower to the uppermost, that is, the glumes, and the first, second, and third lemmas are developed in the order named, though in very close succession (fig. 5). No evidence could be found of the prolongation of the rachilla beyond the uppermost floret. A very noticeable structure of the first and second lemmas is the very much thickened basal region which ends uppermost in a very thin membranous tip. The outer or dorsal layer of cells of these thickened bases have thin walls, and are very much larger than the inner denser cells (fig. 6). The rachilla disarticulates just above the glumes. At the point of disarticulation, the rachilla is very small, and it seems possible that the layer of large cells of the sterile lemmas by hygroscopic action may function in the ejection of the

caryopsis. The caryopses have been observed disconnected and lodged between the upper ends of the two glumes.

The panicle of *Phalaris arundinacea* is open during anthesis, after which it is closed, forming a long cylindrical contracted panicle. The lanceolate spikelets are included by two wingless glumes. What has been said with reference to the structure of *P. canariensis* applies likewise to *P. arundinacea* (fig. 7). The two lower lemmas probably show more of a tendency to be reduced to bristles above the much thickened basal portions (fig. 8). These basal regions also show the single layer of much enlarged cells on the dorsal side. The lower members of the spikelet are developed earlier than the upper as in the preceding species.

In *Anthoxanthum odoratum* (fig. 9) the unequal glumes enclose, besides the perfect terminal floret, two hairy, bifid, dorsally awned lemmas (fig. 10). These lemmas show evidence of having an undeveloped floret in the axil of each (fig. 11). The perfect terminal floret has but two stamens, no lodicules, and usually a two-parted plumose stigma. In the development of the spikelets of this species it is found that it agrees with the two species of *Phalaris* in the order of the development of the parts, the lower members appearing earlier than the upper (fig. 11). Here again is found the layer of enlarged cells on the ventral side of the first and second lemmas.

The open panicle of *Torresia odorata* is composed of three-flowered spikelets (figs. 12, 14), with the terminal floret perfect and the two lower florets staminate or frequently empty. In the terminal and in the lower florets, when the latter are developed, are found three stamens. In dissecting the spikelets just before anthesis it is quite obvious that the lower florets are more advanced than the upper (fig. 13). Material for a more detailed study of sections was not available in time for this paper, but the order of development of the spikelet is very evident from the spikelets which were dissected just before anthesis, and is found to agree with the other three species described (fig. 13). Sections were not necessary in this case to ascertain whether the spikelet is more than one-flowered since the first and second lemmas show fully developed staminate flowers in their axils.

ANOMALIES

Some anomalies were observed in some of the specimens which were dissected. In a few cases in *Phalaris canariensis* and *Torresia odorata* spikelets were found in which the two filaments of the two lateral stamens were united into one for two thirds of the distance up from the base but were distinct at the top with an anther on each (figs. 15, 16). In *Anthoxanthum odoratum* and in *Torresia odorata* (fig. 17) instances were noted in which the stigmas were three-parted.

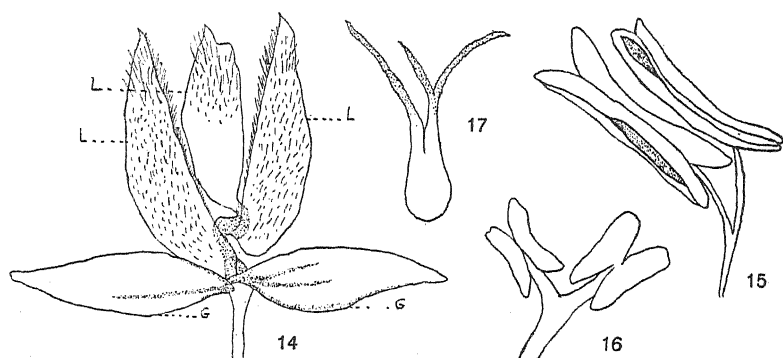


Fig. 14. *Torresia odorata*. Spikelet with glumes pulled apart, showing the three enclosed florets. $\times 3.7$. G, glume; L, lemma. Fig. 15. *T. odorata*, and fig. 16 *P. canariensis*, showing the united filaments of the lateral stamens. $\times 3$. Fig. 17. *T. odorata*, showing the three-parted stigma. $\times 3$.

DISCUSSION

The three genera are closely comparable in the structure of the spikelet and in the order of the development of its members. The spikelet of *Torresia* clearly shows three flowers fully developed. The flowers in the first and second lemmas, being staminate and more advanced than the uppermost, definitely exhibit an indeterminate condition. In the first and second lemmas of *Anthoxanthum* and *Phalaris* are found evidences of florets which do not develop very far, and in each of these species it is found from sections made of early stages that the lower members of the spikelet are more advanced than the upper; therefore all of them show the same indeterminate condition.

It is found that the spikelet of *Anthoxanthum* differs from the other species in the absence of lodicules and in that the perfect, uppermost floret has but two stamens, but agrees in all other features very strikingly with the other three species here described.

A prolongation of the rachilla beyond the uppermost floret could not be observed in any of the sections made in any of these species, although Mrs. Arber (1925) reports having found a definite prolongation of the rachilla in the genus *Ehrharta* of this tribe.

The following similarities in these species are observed and may be used as a basis of comparison: (1) that each has a spikelet which is morphologically more than one-flowered, (2) that in each the order of development of the members of the spikelet is the same—the lower members developing first, and (3) that it is the uppermost spikelet in each case which is the perfect one with the incomplete or aborted florets below.

Lamb attempted to overcome the difficulties of present classifications, and his method based on what he considered the evolution of this family is a tendency in the right direction; but the basis which he selected, that of the relative position of the large and small flowers of the spikelet does not present a phylogenetic relationship. However, it is believed that a morphological study and comparison of the order of development of the spikelet does present phylogenetic relationships which can be used as a basis for classifying the Gramineae.

If, in classifying the Gramineae, we use as a basis the structure of the spikelet and the order of development of the members of the spikelet, we can say that these species, judging from the similarities enumerated above, constitute a distinct group. Upon this basis it is possible to group the Phalarideae with the Poatae without making them an exception, and it seems possible to divide all the Gramineae having more than one flower in the spikelet on this basis without the necessity of making exceptions. Such a basis has already been pointed out by Weatherwax (1923), who states that

A sharp line of distinction may be drawn between one group of genera, in which the spikelet is indeterminate, and another in which it is determinate. In the one the lower flower is most advanced in development, and abortion is most likely to occur at the top; in the other, this order is reversed.

Though in an indeterminate inflorescence the abortion of parts is most likely to occur at the top, yet in Phalarideae the abortion has occurred below the developed floret. However, the order of development still holds, for the lower members are the most advanced.

On this basis those species of Gramineae which have more than one flower in the spikelet may be divided into two groups: (1) those genera in which the spikelet is more than one-flowered and determinate; and (2) those in which the spikelet is more than one-flowered but indeterminate. The Phalarideae, then, being more than one-flowered and indeterminate, would thus be classed with the latter group.

SUMMARY

1. The tribe Phalarideae has never consistently fitted in with the classifications which have been made of the Gramineae, due to the fact that it was judged only by characters which are external. It is here suggested that the remedy is to be looked for in the better use of the morphological characters to emphasize phylogenetic relationships.

2. Through a morphological study of the development of the spikelets it is found that the Phalarideae form a definite group, in that they have in common a spikelet with a perfect terminal flower, that they have more or less evidence of rudimentary flowers in the axils of the lower lemmas, and the spikelets all develop in the same order—the lower members being the more advanced.

3. On the basis of the order of the development of the florets in the spikelet, the Gramineae having more than one flower in the spikelet may be divided into two groups: the Panicatae with determinate inflorescence, and the Poatae with indeterminate inflorescence. With this fundamental division of the family, we can consistently place the tribe Phalarideae in the Poatae without making it an exception.

The writer wishes to express his appreciation of the criticism and suggestions of Dr. Paul Weatherwax who suggested the problem, and under whose direction this work was done in the laboratories of Indiana University.

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Explanation of plates 20, 21

PLATE 20

Figs. 1-6. *Phalaris canariensis*.

- Fig. 1. Whole spikelet. $\times 7$.
Fig. 2. Spikelet with glumes removed. $\times 7$. *L*, lemma.
Fig. 3. Longitudinal section of the spikelet. $\times 7$.
Fig. 4. Cross section of the spikelet. $\times 25$. *L*, lemma; *G*, glume; *R*, rudimentary floret.
Fig. 5. Longitudinal section of young spikelet showing the order of development. $\times 25$. *G*, glume; *L*, lemma; *P*, palea.
Fig. 6. Longitudinal section of empty lemma showing enlarged cells on the dorsal side. $\times 6$.
Fig. 7. *P. arundinacea*. Longitudinal section of the spikelet. $\times 6$.

PLATE 21

Fig. 8. *P. arundinacea*. Spikelet with glumes removed. $\times 6$. *G*, glume; *L*, lemma; *R*, rudimentary floret; *P*, palea; *Pi*, pistil; *St*, stamen.

Figs. 9-11. *Anthoxanthum odoratum*.

Fig. 9. A spikelet. $\times 3$ *G*, glume; *L*, lemma; *A*, awn of lemma; *Pi*, stigmas of pistil.

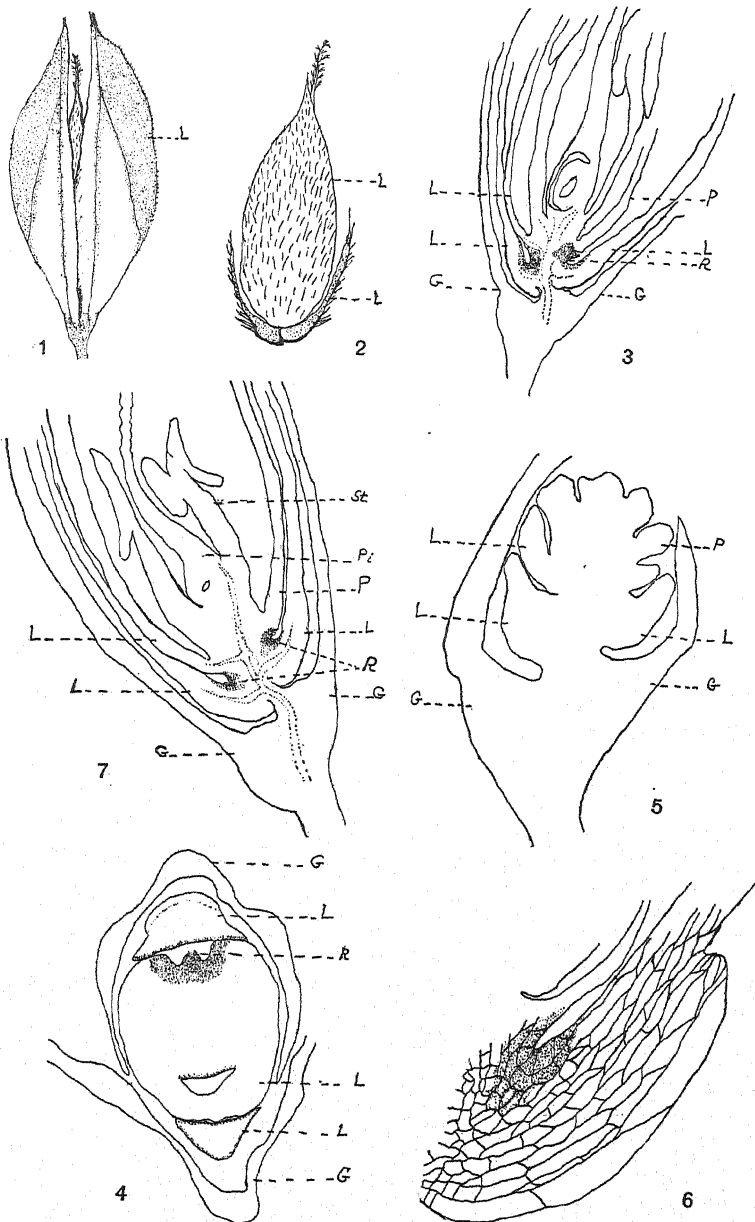
Fig. 10. Two spikelets, the upper one with glumes removed. $\times 3$.

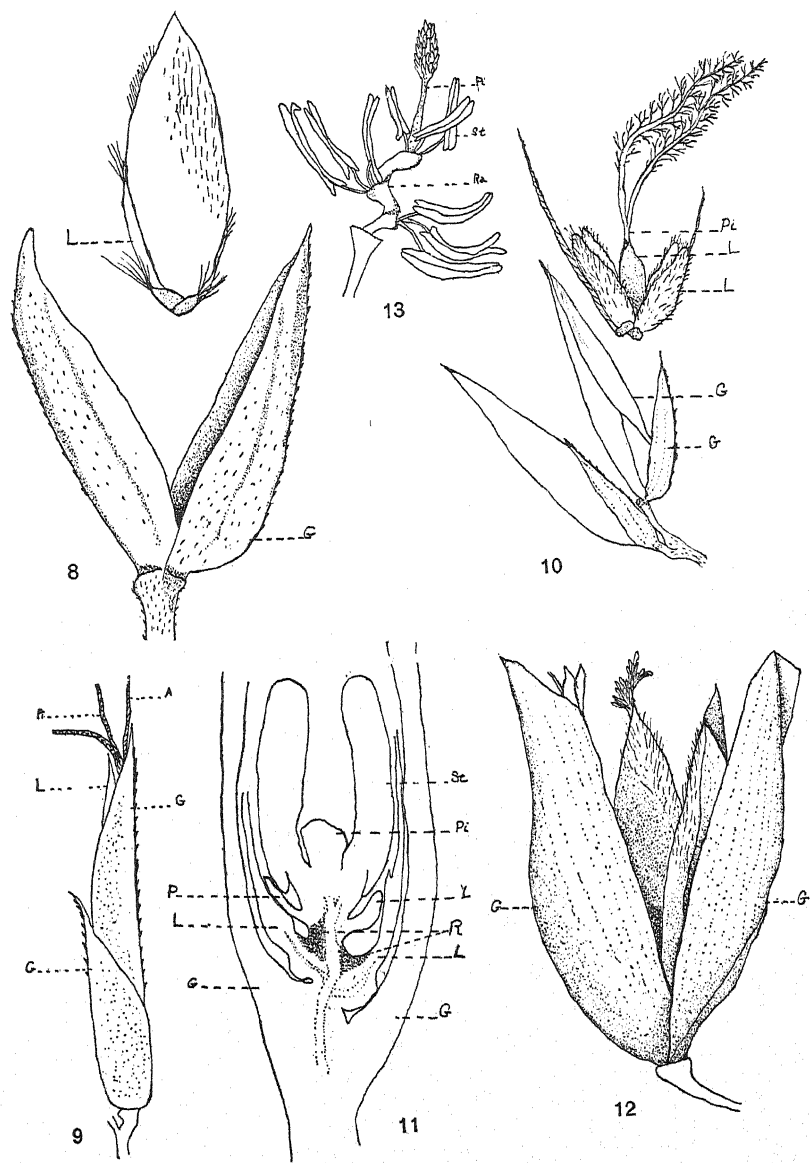
Fig. 11. Longitudinal section. $\times 3$. *G*, glumes; *L*, lemma; *R*, rudimentary florets; *P*, palea; *Pi*, pistil; *St*, stamen.

Figs. 12, 13. *Torresia odorata*.

Fig. 12. A spikelet. $\times 3$.

Fig. 13. Spikelet showing only the essential organs; lower florets more advanced. $\times 3.7$. *St*, stamen; *Pi*, pistil; *Ra*, rachilla.





Fresh water algae from the Green River formation of Colorado

WILMOT H. BRADLEY¹

(WITH PLATES 22, 23)

In the writer's investigation of the origin of the group of lake beds of Colorado, Utah, and Wyoming, known as the Green River formation, a systematic study of the microfossils was made in addition to the geologic studies, in order to aid in interpreting the conditions that prevailed in the ancient lake. This lake existed for several million years during the middle part of the Eocene epoch, which is the earliest epoch of the Tertiary Period. Although the Eocene represents a rather late epoch in the earth's history, rocks formed during the middle of that epoch are probably of the order of forty million years old. The complete report on this investigation will be published by the United States Geological Survey.² Professor Gilbert M. Smith, of Stanford University, criticized the parts of that manuscript describing the algae and offered very helpful suggestions concerning the analogy between them and certain living forms. Later, when the writer published the descriptions and figures of a few of these fossil algae in a brief paper (Bradley, 1929) bearing on the interpretation of certain disputed structures in other oil shale deposits, Professor Smith³ suggested that as these fossil algae might be of as much interest to botanists as to geologists it would be desirable to publish descriptions of some of them in a journal that circulates chiefly among botanists. This paper was prepared in accordance with that suggestion. The writer wishes to express here also his appreciation to Professor Smith for his thorough criticism and generous help.

OCCURRENCE

Because these algae were fossilized in a manner different from that of most fossils, a brief consideration of their occurrence will assist to explain the preservation of such delicate and normally ephemeral organisms. The Green River formation

¹ Published by permission of the Director, U. S. Geological Survey.

² BRADLEY, W. H. The origin and microfossils of the oil shale in the Green River formation of Colorado and Utah. U. S. Geo. Surv. Prof. Paper (in preparation).

³ Personal communication, July, 1929.

consists chiefly of thinly laminated beds of marlstone that contain a relatively small quantity of organic matter. Associated with the marlstone beds are groups of oil shale beds which are in reality only marlstone and shale beds with an extraordinarily large proportion of organic matter. All of these beds were laid down in a large and comparatively shallow lake which for a large part of its life was essentially a fresh water body. The beds considered here, therefore, are simply compacted and lithified lacustrine oozes and the organic matter they contain was derived predominantly from minute aquatic organisms that inhabited the lake. It is in the richest beds of oil shale or in other words in those that contain the greatest proportion of organic matter that the fossil algae described here were found.

Most of the thin sections of these organic rocks were ground in the same way that ordinary rock sections are cut. Others, however, were cut in a microtome after the mineral matter had been removed and the organic matter softened in hot concentrated phenol.

Two kinds of organic matter can be clearly distinguished in the thin sections. One is entirely structureless, translucent, and lemon-yellow to reddish-brown. It makes up the ground-mass of the rock and contains various quantities of finely divided mineral matter. The other kind of organic matter consists of complete or fragmentary organisms such as algae, fungi, protozoa, insects, and parts of higher plants, as spores, pollen grains, or minute pieces of tissue.

Chroococcus? sp. cf. *C. Westii* (W. West) Boye, P. (plate 22, fig. 1). This fossil alga seems to belong to the Chroococcaceae. All the individuals consist of a pair of broadly ovate semicells that range from 12 to 18.5 microns in diameter. The cell walls are thick and homogeneous. Sheaths are apparently absent though originally they may have been present and have merely contracted and merged with the cell wall thus making it appear somewhat thicker. The shape and size of these cells agree very well with the living *C. Westii*. The cells of *C. Westii*, without the sheaths, range from 13 to 27 microns in diameter (Geitler, 1925 p. 78, fig. 70). The reticulate system of shrinkage cracks, which are unmistakable under the microscope, lend the fossil a superficial resemblance to certain sculptured dinoflagellates.

The microflora of the Green River oil shale contains more individuals of this species than any other. In one specimen the writer calculated that there were about 5700 individuals per cubic centimeter. This calculation, though subject to large errors, is probably of the right order of magnitude.

Crinalium? sp. cf. *C. endophyticum* Crow (fig. 2). These strap-shaped filaments are much like those of Crow's genus *Crinalium* (Crow, 1927). They are duplex, slightly twisted, and without apparent transverse septa. Moreover, some of them are sharply bent in the middle, though none are really U-shaped. They differ from *C. endophyticum* in that they are nearly 7 microns broad, whereas the filaments of the living species are 3 to 4 microns in diameter. Like other fossil algae of this micro-flora no sheath is discernible and it is impossible to tell if there ever was one. Filaments like these are common in the oil shale and all are much broken by shrinkage cracks.

Hapalosiphon sp. cf. *H. confervaceus* Borzi (fig. 3). This alga is remarkably suggestive of certain living species of *Hapalosiphon*, yet it does not agree exactly with any of them. It comes closest to *H. confervaceus* Borzi, but differs in being slightly smaller and in not having its filaments coated with small grains of calcium carbonate as described by Geitler (1925, p. 201). The trichomes of *H. confervaceus* range from 15 to 22 microns in diameter, whereas those of the fossil range from 11 to 13 microns. Moreover, no sheath is discernible in the fossil alga and it is impossible to tell if it ever had one. The fossil also resembles *H. aureus* W. and G. S. West, but is more richly branched and the branches are about the same size as the principal filament rather than smaller. *H. flexuosus* Borzi has all the characters of the fossil, but is considerably smaller. Its trichomes average 6-8 microns in diameter.

Phacus sp., cf. *P. caudata* Hübner (plate 23, fig. 4). This pyriform cell is remarkably like certain species of the euglenoid genus *Phacus*. The short, straight caudal spine, the asymmetry of the forward end, and the dimensions are very close to *P. caudata* Hübner, which is 22.5 microns wide and 45 microns long (Lemmermann, 1913). The fossil is about 25 microns wide and 46 microns long. However, no longitudinal striae and no longitudinal fold are discernible, though these characters may have been obscured during compaction and lithification of the

ooze in which the organism was embedded. The fossil is also very nearly like *Lepocinclis teres* (Schmitz) Francé, especially in the shape and length of the spine, but this living species is symmetrical. This fossil is remarkable in that it apparently represents the preservation of a naked protoplast. In commenting upon this fossil Professor Smith⁴ called the writer's attention to a central light dot in just the position of the paramylon-grain of *Phacus*. Examination in polarized light shows that this dot is due to the presence of a minute mineral grain which only by chance happens to occupy the position of the paramylon-grain.

Tetraedron sp. cf. *T. regulare* var. *torsum* (Turner) Brunnthaler (fig. 5). This alga shows a striking resemblance to the living *Tetraedron regulare* var. *torsum*. It is excellently preserved and shows no shrinkage cracks. It is brownish-orange and although clear and translucent it is somewhat darker than the groundmass. The alga appears to be perfectly homogeneous and all differentiation between the cell wall and contents has disappeared.

Coelastrum? sp. cf. *C. verrucosum* Reinsch (or *Pediastrum?* sp.) (fig. 6). This group of cells which the late Charles A. Davis (1916) regarded either as a *Pediastrum* or a member of a closely related genus may be a *Coelastrum*. It is somewhat similar to *C. verrucosum* Reinsch. According to this interpretation this group of eight cells represents a flattened and partly fragmented coenobium whose cells were more or less rounded and lobed. The individual cells of *C. verrucosum* (Reinsch 1877) are about 9.7 microns in diameter, whereas those of the fossil measure about 10 microns across. But the irregular lobes on the cells of the fossil are apparently more rounded and larger in proportion to the size of the cell than the irregular wart-like prominences on the cells of *C. verrucosum*. Nevertheless, the number of the cells, their size, and general aspect are nearly enough like *C. verrucosum* to warrant the suggestion that the fossil may be a species of *Coelastrum* comparable to *C. verrucosum* Reinsch.

Microspora sp. cf. *M. pachyderma* (Wille) Lagerheim (fig. 7). This alga, which is represented in the microflora of the Green River formation by a single fragment, is very close to *M.*

⁴ Personal communication, Jan., 1928.

pachyderma in filament structure, cell shape, and dimensions. The filament of the fossil is about 16.5 microns in diameter and the cells average 13.5 microns in diameter and 20 microns long. The cells of *M. pachyderma* are 9 to 12 microns in diameter and 1 to 2 times as long as wide. (Heering, 1914, p. 152).

The color of this fossil is unusual. It is pale lemon-yellow and almost transparent, whereas most of the algae in the oil shale are reddish-yellow, reddish-orange or dark reddish-brown. The color is very close to that of the pollen grains and waxy spore exines found in the oil shale.

Stigeoclonium? sp. cf. *S. lubricum* (Dillwyn) Kützing (fig. 8). It is not at all certain that this fragment of a branching alga belongs here. Too little of the character of the cell contents is known to be sure in the first place whether it is a member of the Chlorophyceae or Cyanophyceae. However, it is placed here provisionally because its manner of branching and the size and shape of the cells are so suggestive of *S. lubricum*. The cells are quadrate or cask-shaped and range in diameter from about 7 to nearly 10 microns. Hazen (1902, p. 196) gives the diameter of the branchlets of *S. lubricum* as 6 to 7 microns and the diameter of the principal filaments as 14 to 16.5 microns. The fossil, which is unusually large compared with other specimens of the microflora, also resembles the blue-green alga *Capsosira* Kützing (see Geitler, 1925, p. 171), but shows no indication of the heterocysts characteristic of this genus, and in its branching and general aspect is more like *Stigeoclonium*.

MANNER OF PRESERVATION

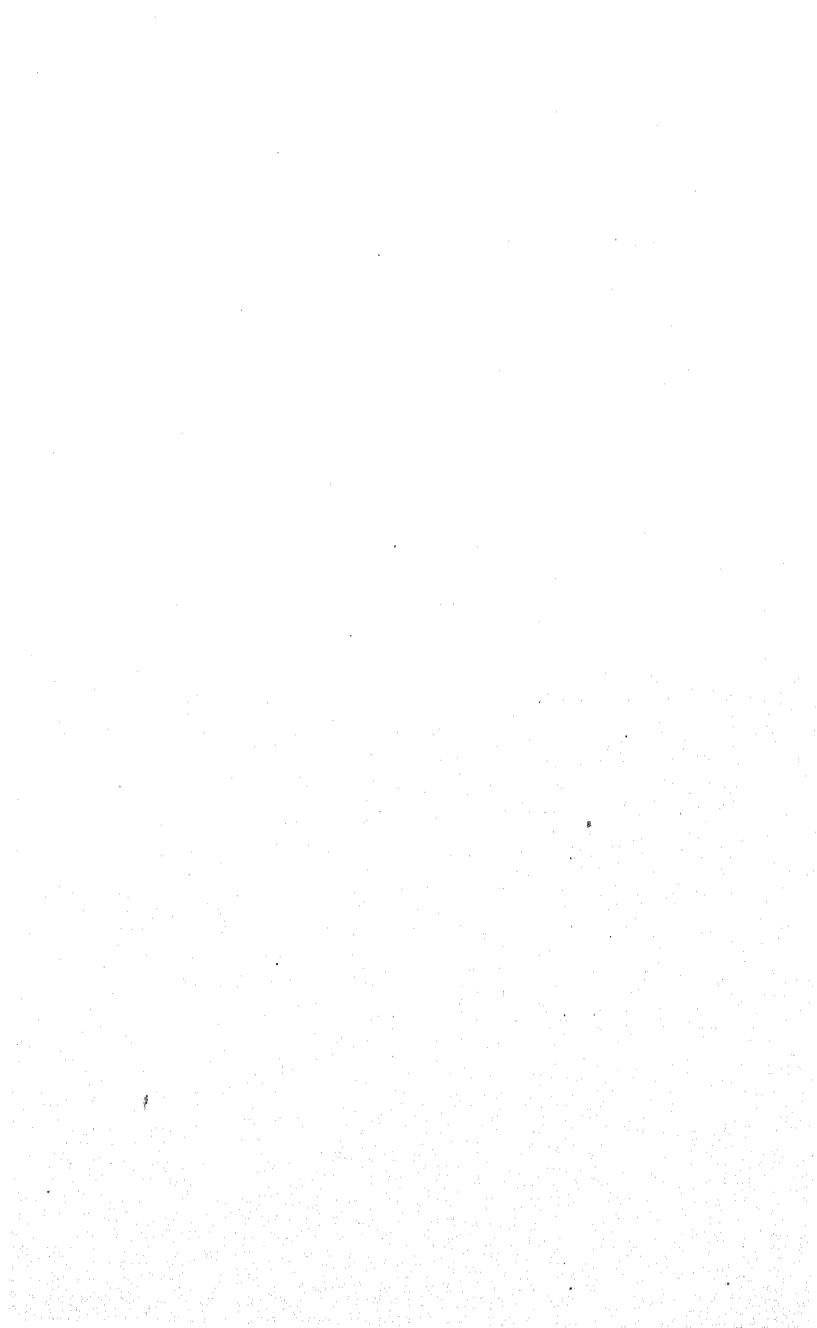
The structureless organic matter in which these and other algae are embedded was derived from the partial decomposition of minute aquatic organisms that dwelt in the ancient lake. It seems probable that planktonic algae furnished the greater part of the original gelatinous ooze but probably other aquatic organisms like protozoa, bacteria, and various insect larvae also contributed. When the decomposition of these organisms reached a certain stage, bacterial activity evidently ceased or was greatly retarded and the resulting gelatinous ooze remained essentially stable and apparently somewhat antiseptic. Comparable deposits of richly organic ooze are known in certain existing lakes. This gelatinous ooze acted as a protecting

medium against the activity of putrefactive bacteria and so preserved delicate organisms like algae and fungi that became accidentally entombed in it. Presumably the cells of these algae were partially impregnated with the ooze in somewhat the same manner that amber penetrated the tissues of its plant inclusions. Thus these algae were supported, or rather, suspended in an agelatinous matrix until the whole mass had become hardened into rock. It appears that many of the algae in the Green River oil shale contained more moisture than the matrix, for they contracted more, and so are broken by numerous shrinkage cracks. (See plate 22, fig. 3).

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Explanation of plates 22, 23

The photomicrographs from which figures 1-3 of plate 22 and figures 6 and 8 of plate 23 were taken were made under the direction of the late Charles A. Davis. The other photomicrographs were taken by the writer.

PLATE 22

Fig. 1. *Chroococcus* sp. cf. *C. Westii* (W. West) Boye, P. The alga shows a reticulating system of shrinkage cracks. $\times 430$.

Fig. 2. *Crinalium?* sp. cf. *C. endophyticum* Crow. The transverse shrinkage cracks in these algae give an erroneous impression of transverse septa. $\times 185$.

Fig. 3. *Hapalosiphon* sp. cf. *H. confervaceus* Borzi. The reticulating system of shrinkage cracks in this alga resemble that in the *Chroococcus*. $\times 375$.

PLATE 23

Fig. 4. *Phacus* sp. cf. *P. caudata* Hüber. The transverse cracks are due to shrinkage. The light dots and angular areas are mineral grains which, together with the fossil, are embedded in the light gray structureless organic matrix of the oil shale. $\times 410$.

Fig. 5. *Tetraedron* sp. cf. *T. regulare* var. *torsum* (Turner) Brunthaler. This alga shows no shrinkage cracks and is embedded in an oil shale whose mineral grains are somewhat coarser than the others. $\times 200$.

Fig. 6. *Coelastrum?* sp. cf. *C. verrucosum* Reinsch (or *Pediastrum?* sp.). These cells show no shrinkage but were probably somewhat distorted during compaction of the sediment. $\times 740$.

Fig. 7. *Microspora* sp. cf. *M. pachyderma* (Wille) Lagerheim. This photomicrograph was taken from a microtome section of the oil shale from which all the mineral grains have been removed. It shows more clearly than the other that the volume of structureless organic matter in these oil shale beds greatly exceeds the mineral matter. $\times 250$.

Fig. 8. *Stigeodinium?* sp. cf. *S. lubricum* (Dillwyn) Kützing. The shrinkage cracks in this alga are small and consequently the transverse walls are more plainly discernible. $\times 410$.



BRADLEY: GREEN RIVER FORMATION ALGAE



BRADLEY: GREEN RIVER FORMATION ALGAE

INDEX TO AMERICAN BOTANICAL LITERATURE 1924-1929

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New physiologic races of the oat smuts¹

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In earlier publications I have described the occurrence of specialized races of both loose (*Ustilago Avenae* (Pers.) Jens.) and covered (*U. levis* (K. & S.) Magn.) smuts of oats, which are distinguished by their different capacity for infecting oat varieties. The evidence recorded in the first paper (Reed, 1924) showed the existence of two distinct races of each of these smuts. The data were secured by the inoculation of several varieties of oats with a collection of each smut from Columbia, Missouri, and a second collection from Aberystwyth, Wales, which was sent to me by Miss Kathleen Sampson. The distinctive behavior of these two smuts was also confirmed by Miss Sampson (1925), who used them for inoculating several varieties of oats at the Welsh Plant Breeding Station. In a second paper (Reed, 1927), specialized races of loose smut which attacked Fulghum and Red Rustproof oats, belonging to the Red Oat Group, were described. These varieties had shown an unusually high degree of resistance to the other races, but Fulghum was severely attacked by collections of smut from Tennessee, Oklahoma, and Texas, and Red Rustproof by a different collection from Texas. Miss Sampson (1929) has recently recorded the occurrence of a new race of loose smut, characterized by its capacity for infecting *Avena brevis* and *A. strigosa*, and has also isolated another race of the covered smut. Rodenhiser (1928) has recorded differences in the cultural characteristics of collections of both loose and covered smut.

During the past few years I have been accumulating additional data on the general problem of physiologic specialization in the smuts of oats. A large number of collections of both loose and covered smuts have been obtained from various sources, and their capacity for infecting oat varieties has been determined. The result has been to demonstrate the existence of a large number of new races which can be distinguished by their varying ability to infect varieties of oats.

Extensive tests with my original collection of loose and covered smut from Missouri have been made on a large number

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of oat varieties (Reed, 1920; Reed, Griffiths, and Briggs, 1925). In the more recent studies, relatively few kinds of oats have been used, but they have served to show the main features of specialization. It is quite possible that if a larger number of varieties were grown in the experiments, additional evidence on the specialization of the various smut collections might be secured.

The methods employed have been similar to those used in previous studies. The inoculated plants have been grown to maturity, both in the greenhouse and in the field. Separate lots of seed were inoculated with the spores of the different smut collections. The inoculated seed was then planted in sand with a soil moisture of 20 per cent of its water-holding capacity, covered to a depth of about one inch, and germinated in a constant-temperature tank at 20°C. Earlier studies (Reed and Faris, 1924) have shown that these environal conditions are very favorable for securing high percentages of infection with the oat smuts. In most of the experiments, twenty seeds were planted in each container. The seedlings emerged ordinarily in four days and soon thereafter were transplanted to the greenhouse benches or to the field, where they were grown to maturity.

In most cases, two or more different experiments were carried out with each smut collection. Generally one or more series was carried to maturity in the greenhouse, and others in the field. The results, however, are combined in the tables. Since twenty seeds were usually inoculated in each experiment, the number of plants recorded in the tables indicates, to some extent at least, the number of different tests which were made with a particular variety and collection of smut.

It was usual to obtain high percentages of infection with varieties susceptible to a particular collection of smut. An examination of the tables will reveal the fact that frequently one hundred per cent of the inoculated plants were smutted. Every collection of each smut gave these high percentages with one or more oat varieties. Evidently favorable conditions for infection were secured, and thus the evidence for the specialization was conclusive.

In a number of the experiments only an occasional infected plant of a variety was observed. This may be accounted for

in different ways. For one thing, it is possible that an occasional seed was contaminated with smut from some unknown source. The fact that several collections of smuts were grown more or less adjacent to each other may account for some possible contamination. The second possibility is that an occasional stray seed of some variety was accidentally mixed with another and used in the planting. Usually, there was no way of detecting such mixtures, since the heads and grain of the infected plants were destroyed. There is also the third possibility that a resistant variety may, under exceptionally favorable conditions, be infected by a race of smut which ordinarily does not attack it. In a few cases we have conclusive evidence of this fact, since careful experiments have been tried out in which there was no possibility of accidental contamination of the seed or accidental mixtures of varieties.

PHYSIOLOGIC RACES OF *USTILAGO AVENAE*

The data for fifteen collections of loose smut are recorded in tables 1 to 5. In the tables 2 to 5 there are given the detailed results of the number of plants inoculated, the number infected and the percentage infected, while in the first table the combined results are given in order to show the peculiar behavior of the different varieties. One or more varieties or strains of seven different species of the genus *Avena* are included in these experiments, and the results indicate clearly the existence of a large number of specialized races of the loose smut.

A few general statements regarding the reaction of the different varieties to these collections of loose smut may be made. *Avena barbata* has proved to be exceedingly susceptible to all the collections with which it has been tested. Twelve of the fifteen collections have been used to inoculate this species, and in most cases one hundred per cent infection has been secured. The lowest percentage was obtained with Collection No. 4, in which 31 out of 49 plants (63.2 per cent) were infected.

One strain of *Avena brevis* was inoculated with all of the fifteen collections, and in every case proved to be entirely resistant; no infected plants were observed in any of the experiments.

Among the varieties of *Avena sativa*, two—Black Mesdag and Markton—stand out as completely resistant. Black Mes-

dag was tested with all fifteen collections, and Markton with all of them except No. 3, and no infected plants of either of these varieties were obtained in any of the experiments.

TABLE 1

Summary of results with *Ustilago Avenae* (Pers.) Jens.^a

SPECIES AND VARIETY	SEED NO.	PHYSIOLOGIC RACE											COLLECTION NUMBER					
		I	II	III	IV	V	VI	VII	VIII	IX			X	XI				
		Missouri	France	Kansas	France	Tunis	Germany	England	Germany	Wales	France	Tennessee	Oklahoma	Texas	Texas	France		
		1	5	16	6	11	9	8	10	7	4	12	13	14	15	3		
<i>Avena barbata</i> Brot.....	830	5	5	—	—	5	—	5	5	5	4	5	5	5	4	5		
<i>Avena brevis</i> Roth.....	289	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Avena nuda</i> L.....																		
Hull-less.....	30	5	5	4	4	4	5	5	2	1	1	5	4	4	0	0		
Liberty.....	292	5	4	5	5	4	5	5	0	0	0	2	2	3	0	—		
<i>Avena orientalis</i> Schreb.....	246	5	5	0	1	0	0	0	0	1	0	1	3	3	0	—		
Green Mountain.....	110	5	5	5	5	5	5	0	1	0	0	—	—	—	—	—		
<i>Avena sativa</i> L.....																		
Bicknell.....	341	2	1	—	1	4	1	1	1	1	1	5	3	5	1	—		
Black Diamond.....	116	5	5	5	1	2	0	1	1	2	2	5	4	5	1	—		
Black Mesdag.....	70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Black Norway.....	118	4	5	1	4	5	5	5	5	1	0	—	—	—	—	—		
Canadian.....	119	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1		
Early Champion.....	150	5	5	5	3	4	4	2	4	1	3	—	—	—	—	—		
Early Gothland.....	152	5	4	1	1	0	0	1	0	1	0	0	3	3	0	0		
Green Russian.....	316	4	3	5	0	0	0	0	0	1	0	0	0	1	2	—		
Joanette.....	187	0	0	5	3	0	0	0	0	1	4	0	0	0	0	—		
Markton.....	752	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—		
Monarch.....	161	1	1	5	3	2	1	1	1	1	2	2	3	1	0	0		
Monarch Selection.....	162	5	3	5	2	0	1	0	0	0	1	1	—	—	—	—		
Nebraska No. 21.....	280	4	4	4	0	1	1	0	0	0	0	0	1	1	0	—		
Rossman.....	322	5	3	0	1	0	0	1	0	1	1	0	2	1	—	—		
Scottish Chief.....	124	3	3	4	3	4	4	3	0	1	0	1	2	1	0	0		
Trisperma.....	64	5	4	5	5	5	5	5	4	0	0	4	1	3	0	—		
Victor.....	126	5	5	5	5	5	5	5	5	5	5	5	3	4	1	2		
<i>Avena sterilis</i> L.....																		
Burt.....	175	1	1	0	0	0	1	1	0	0	0	1	1	1	1	—		
Fulghum.....	129	1	0	—	0	0	1	0	0	1	0	4	4	4	0	0		
Navaro.....	946	0	—	—	—	—	—	—	—	—	—	0	0	0	0	—		
Red Rustproof.....	131	0	0	0	0	0	0	1	0	0	0	0	0	0	4	0		
<i>Avena strigosa</i> Schreb.....	587	2	0	0	0	1	0	1	0	0	0	0	0	0	—	0		

^a In the body of this table numerals are used as symbols with the following significance:

—=No trial

2=11-25 per cent

5=75-100 per cent

0=No infection

3=26-30 per cent

1=1-10 per cent

4=51-75 per cent

The other oat varieties inoculated gave quite different results with the various collections of smuts, and thus served to differentiate the specialized races.

Race I is based upon Collection No. 1. The original collection was made many years ago near Columbia, Missouri, and has been used in extensive experiments year after year. Its capacity for infecting a large number of varieties of oats

belonging to the various species has been determined, and most of them are more or less susceptible to this race of smut, relatively few being resistant (Reed, 1920; Reed, Griffiths, and Briggs, 1925). It has also been used in the earlier studies of physiologic specialization (Reed, 1924, 1927).

In the present experiments, only a few varieties or strains which seemed to be significant for the present purposes were included in the tests. Two varieties belonging to *Avena nuda*

TABLE 2
Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED NO.	Avenae No. 1 Missouri			Avenae No. 5 France			Avenae No. 16 Kansas		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
<i>Avena barbata</i> Brot.	830	38	38	100.0	18	17	94.4	—	—	—
<i>Avena brevis</i> Roth.	289	84	0	0	53	0	0	20	0	0
<i>Avena nuda</i> L.										
Hull-less.	30	126	116	92.0	96	75	78.1	37	27	72.9
Liberty.	292	18	17	94.4	18	12	66.6	18	15	83.3
<i>Avena orientalis</i> Schreb.	246	104	102	98.0	71	54	76.0	37	0	0
Green Mountain.	110	18	18	100.0	18	18	100.0	14	14	100.0
<i>Avena sativa</i> L.										
Bicknell.	341	83	17	20.4	36	1	2.7	—	—	—
Black Diamond.	116	52	46	88.4	14	14	100.0	17	15	88.2
Black Mesdag.	70	102	0	0	78	0	0	20	0	0
Black Norway.	118	53	30	56.6	19	18	94.7	16	1	6.2
Canadian.	119	149	148	99.3	101	88	87.1	39	39	100.0
Early Champion.	150	20	20	100.0	37	37	100.0	39	39	100.0
Early Gothland.	152	127	121	95.2	77	51	66.2	40	1	2.5
Green Russian.	316	55	34	61.8	35	15	42.8	20	19	95.0
Joanette.	187	65	0	0	35	0	0	39	34	87.1
Markton.	752	50	0	0	47	0	0	20	0	0
Monarch.	161	145	1	0.6	93	2	2.1	55	51	92.7
Monarch Selection.	162	53	47	88.6	40	20	50.0	39	33	84.6
Nebraska No. 21.	280	43	31	72.0	52	29	55.7	38	25	65.7
Rossman.	322	58	57	98.2	43	20	46.5	20	0	0
Scottish Chief.	124	125	39	31.2	76	36	47.3	40	27	67.5
Trisperma.	64	62	52	83.8	27	16	59.2	18	15	83.3
Victor.	126	106	105	99.0	76	59	77.6	20	20	100.0
<i>Avena sterilis</i> L.										
Burt.	175	52	2	3.8	44	2	4.5	10	0	0
Fulghum.	129	87	3	3.4	57	0	0	—	—	—
Navarro.	946	17	0	0	—	—	—	—	—	—
Red Rustproof.	131	98	0	0	63	0	0	18	0	0
<i>Avena strigosa</i> Schreb.	587	94	19	20.2	76	0	0	18	0	0

were inoculated, and both proved to be highly susceptible. The same is true of the two varieties of *A. orientalis*. Seventeen varieties of *A. sativa* have been grown in the various experiments. In addition to Black Mesdag and Markton, two others stand out as distinctly resistant, namely, Joanette and Monarch. No infected plants of the former have been observed, while only one, in a total of 145 of the latter, has been obtained. The other varieties used have given comparatively high percentages of infection, the lowest being secured with Bicknell

(17 infected plants out of a total of 83, or 20.4 per cent) and Scottish Chief (39 infected plants out of a total of 125, or 31.2 per cent).

This race has shown very slight capacity for infecting the varieties of the Red Oat Group, tests having been made with Burt, Fulghum, Navarro and Red Rustproof. Usually, entirely negative results have been secured, but occasionally a plant of Burt and Fulghum has been infected. The varieties of this group, however, stand out as strikingly resistant to this race of smut.

Several varieties of *Avena strigosa* have been tested with this race, but only one of them, belonging to the subspecies *glabrescens*, has been used in comparison with the other collections of loose smut. This strain has given very variable results with this race. In one experiment, a relatively high percentage of infection was obtained, while in four others, negative results were secured.

Another collection of loose smut, No. 5, has given results which closely parallel those just described. The original material of this collection was obtained by Dr. C. R. Hursh in June 1924 near Noisy de Roi, France. It has been tested out on all of the species and varieties except Navarro, and its behavior corresponds very closely with that of Collection No. 1. The only obvious difference is its failure to infect Bicknell and *Avena strigosa*. With the former variety, two tests were made in the field and only one plant out of 36 was infected. However, under similar conditions, Collection No. 1 gave practically negative results on this same variety. Four tests have been made with *A. strigosa*, and in no case did any infection occur. On the other varieties and species the collection behaved like No. 1.

Race II is based on Collection No. 16. The material was collected at Hays, Kansas, in 1925 by Mr. F. A. Coffman and forwarded to me by Mr. T. R. Stanton. Office of Cereal Crops and Diseases, U. S. Department of Agriculture. According to the original information, the smut was collected on the Burt oats. The smut, however, has shown no special capacity for infecting Burt oats or other varieties belonging to the *Sterilis* Group. However, the number of tests and plants of these varieties grown in the experiments was quite small.

The smut, however, stands out clearly from Race I. It infects severely both varieties of *Avena nuda* and Green Mountain, a Side Oat type, the other variety of this group giving entirely negative results. Three varieties of *A. sativa*, in addition to Black Mesdag and Markton, namely, Black Norway, Early Gothland, and Rossman, gave practically negative results. The other varieties tested usually gave high percentages of infection.

From the positive standpoint, the outstanding features of this race are its capacity to infect Joannette and Monarch, two varieties completely resistant to Race I. With Joannette, 34 out of 39 plants (87.1 per cent) and with Monarch, 51 out of 55 plants (92.7 per cent) were infected. On the negative side, as already noted, it has failed to infect such varieties as Orientalis (Seed No. 246), Black Norway, Early Gothland, and Rossman, varieties which have usually given very high percentages of infection with Race I. *Avena strigosa* has also given entirely negative results.

Race III is based on Collection No. 6. The material was originally collected by Dr. Hursh in the same locality as collection No. 5. The evidence is clear, however, that it is a distinct race. It has proved capable of infecting both varieties of Hull-less oats. It has also severely infected Green Mountain, but the other Side Oat type gave practically negative results. Among the varieties of *Avena sativa* some, as Early Gothland, Green Russian, Nebraska No. 21, and Rossman, gave practically no infection; other varieties, as Bicknell, Black Diamond, Early Champion, Monarch Selection, and Scottish Chief, gave relatively few infected plants. Severe infection of Joannette and Monarch was secured, and in this respect the race corresponds with the one previously described. It differs from this race, however, in its ability to infect Black Norway and also in giving practically negative results on Black Diamond. The varieties belonging to *A. sterilis* and *A. strigosa* all have proved to be resistant to it.

Race IV is based on Collection No. 11. This was originally secured from contaminated oat seed received from Tunis. It also produces severe infection on the two varieties of the Hull-less Group and the Side Oat, Green Mountain. It is negative on Orientalis (Seed No. 246) and also on Early Goth-

land, Green Russian, Joannette, Monarch Selection, and Rossman. It has severely infected Bicknell, Black Norway, Canadian, Early Champion, Scottish Chief, Trisperma, and Victor; Black Diamond, Monarch, and Nebraska No. 21 gave comparatively low percentages of infection. It has also proved negative on the varieties of the *Sterilis* Group and *Avena strigosa*. It is very similar to Race II; it differs, however, in infecting much more severely Bicknell, less severely Monarch, and not at all infecting Joannette.

TABLE 3

Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED No.	Avenae No. 6 France			Avenae No. 11 Tunis			Avenae No. 9 Germany			Avenae No. 8 England		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
<i>Avena barbata</i> Brot. . . .	830	—	—	—	15	15	100.0	—	—	—	25	25	100.0
<i>Avena brevis</i> Roth. . . .	289	36	0	0	50	0	0	34	0	0	79	0	0
<i>Avena nuda</i> L.													
Hull-less	30	83	44	53.0	99	52	52.5	81	65	80.2	147	113	76.8
Liberty	292	18	14	77.7	19	12	63.1	18	14	77.7	20	18	90.0
<i>Avena orientalis</i> Schreb. .	246	91	1	1.0	66	0	0	65	0	0	85	0	0
Green Mountain	110	18	17	94.4	18	18	100.0	18	18	100.0	16	0	0
<i>Avena sativa</i> L.													
Bicknell	341	30	3	10.0	39	27	69.2	32	1	3.1	29	1	3.4
Black Diamond	116	34	3	8.7	15	2	13.3	16	0	0	38	1	2.6
Black Mesdag	70	71	0	0	69	0	0	54	0	0	126	0	0
Black Norway	118	19	14	73.6	19	15	78.9	19	15	78.9	18	16	88.8
Canadian	119	90	88	97.7	99	93	93.9	69	69	100.0	137	134	97.8
Early Champion	150	39	12	30.7	40	30	75.0	36	26	72.2	37	4	10.8
Early Gothland	152	99	1	1.0	71	0	0	57	0	0	127	2	1.5
Green Russian	316	49	0	0	35	0	0	28	0	0	55	0	0
Joannette	187	40	17	42.5	37	0	0	37	0	0	36	0	0
Markton	752	57	0	0	39	0	0	46	0	0	42	0	0
Monarch	161	91	39	42.8	94	13	13.8	62	2	3.2	128	5	3.9
Monarch Selection . . .	162	38	5	13.1	38	0	0	38	2	5.2	39	0	0
Nebraska No. 21	280	48	0	0	51	4	7.8	48	4	8.3	51	0	0
Rossman	322	40	1	2.5	40	0	0	39	0	0	34	1	2.9
Scottish Chief	124	96	34	35.4	71	47	66.1	78	57	73.0	117	55	47.0
Trisperma	64	28	28	100.0	20	19	95.0	22	22	100.0	14	12	85.7
Victor	126	74	70	94.5	72	56	77.7	54	49	90.7	100	93	93.0
<i>Avena sterilis</i> L.													
Burt	175	61	0	0	46	0	0	35	3	8.5	53	1	1.8
Fulghum	129	79	0	0	76	0	0	58	1	2.6	131	0	0
Red Rustproof	131	76	0	0	34	0	0	53	0	0	111	1	0.9
<i>Avena strigosa</i> Schreb. .	587	46	0	0	57	1	1.7	36	0	0	89	4	4.4

Another collection, No. 9, has given results very similar to those obtained with No. 11. It was sent to me originally by Dr. Theo. Roemer, University of Halle, Germany, from material secured at Leipzig, Germany. It differs from the previous collection by its failure to produce a severe infection on Bicknell, otherwise it runs quite close to this collection. It stands out from Race II by its infection of Black Norway and the negative results obtained with Joannette and Monarch.

Race V is based upon Collection No. 8. The original material was sent to me by Dr. George H. Pethybridge, having been collected in August 1924 at Somerset, England. It is very similar to Race IV, but differs distinctly from that one in its inability to infect Green Mountain and Early Champion. These two varieties have usually given high percentages of infection with the races already described. With this race, however, only 4 plants out of 37 of Early Champion were infected, and none out of 16 of the Green Mountain. Practically negative results have been obtained with the oats of the *Sterilis* Group, and only 4 plants out of 89 of *Avena strigosa* have been infected.

Race VI is based upon Collection No. 10. The original material was sent to me by Dr. Roemer, having been made at Dahlem, Germany. The race is distinguished by the fact that it is incapable of producing severe infection of the Hull-less oats. Green Mountain and Orientalis (Seed No. 246) also gave practically negative results. A considerable number of varieties of the *Sativa* Group of oats also proved to be resistant to this race; in fact, it proved to be capable of severely infecting only the varieties Black Norway, Canadian, Early Champion, Trisperma, and Victor. The results were negative on the *Sterilis* varieties and *Avena strigosa*.

Race VII is based upon Collection No. 7. The data recorded in the table were secured from material received from Dr. Pethybridge who, however, obtained it from Miss Sampson in Wales. The smut is identical with that previously used in my experiments and supplied direct by Miss Sampson. The race stands out from those previously described by its failure to infect *Avena nuda* and *A. orientalis*. Many varieties of *A. sativa*, including Bicknell, Black Diamond, Black Norway, Early Champion, Early Gothland, Green Russian, Joannette, Monarch, Monarch Selection, Nebraska No. 21, Rossman, Scottish Chief, and Trisperma, proved to be negative; in fact, only two varieties—Canadian and Victor—showed any high degree of susceptibility to this race. *Avena sterilis* and *A. strigosa* have also given essentially negative results.

Race VIII is based upon another collection, No. 4, made by Dr. Hursh at Lambesc, France, in June 1924, and has given results very similar to those described for Collection No. 7.

It has run fairly parallel to it in its behavior with reference to the varieties. The only outstanding difference is its capacity for infecting Joannette; 26 out of 37 plants (70.2 per cent) of this variety were infected, while only 2 out of 35 plants (5.7 per cent) were infected with the previous collection. Early Champion and Monarch also have given somewhat higher percentages of infection. *Avena sterilis* and *A. strigosa* have proved negative.

TABLE 4
Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED NO.	Avenae No. 10 Germany			Avenae No. 4 France			Avenae No. 7 Wales			Avenae No. 3 France		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
<i>Avena barbata</i> Brot.....	830	15	14	93.3	49	31	63.2	24	24	100.0	36	36	100.0
<i>Avena brevis</i> Roth.....	289	36	0	0	77	0	0	84	0	0	49	0	0
<i>Avena nuda</i> L.....													
Hull-less.....	30	80	12	15.0	125	2	1.6	150	2	1.3	48	0	0
Liberty.....	292	19	0	0	16	0	0	18	0	0	—	—	—
<i>Avena orientalis</i> Schreb.....	246	67	0	0	73	0	0	78	1	1.2	—	—	—
Green Mountain.....	110	14	1	7.1	16	0	0	14	0	0	—	—	—
<i>Avena sativa</i> L.....													
Bicknell.....	341	38	2	5.0	40	1	2.5	30	2	6.6	—	—	—
Black Diamond.....	116	18	1	5.5	19	4	21.0	37	5	13.5	—	—	—
Black Mesdag.....	70	55	0	0	107	0	0	133	0	0	48	0	0
Black Norway.....	118	19	18	94.7	16	0	0	19	1	5.2	—	—	—
Canadian.....	119	70	67	95.7	125	125	100.0	182	175	96.1	49	1	2.0
Early Champion.....	150	36	19	52.7	37	13	35.1	39	1	2.5	—	—	—
Early Gothland.....	152	69	0	0	98	0	0	141	1	0.7	27	0	0
Green Russian.....	316	35	3	8.5	35	0	0	44	0	0	—	—	—
Joannette.....	187	38	0	0	37	26	70.2	35	2	5.7	—	—	—
Markton.....	752	56	0	0	43	0	0	51	0	0	—	—	—
Monarch.....	161	73	5	6.8	118	22	18.6	151	1	0.6	41	0	0
Monarch Selection.....	162	38	0	0	40	3	7.5	56	2	3.5	—	—	—
Nebraska No. 21.....	280	54	0	0	51	0	0	51	0	0	—	—	—
Rossman.....	322	38	0	0	39	1	2.5	40	3	7.5	—	—	—
Scottish Chief.....	124	74	0	0	96	0	0	142	1	0.7	19	0	0
Trisperma.....	64	24	17	70.8	29	0	0	20	0	0	—	—	—
Victor.....	126	62	53	85.4	85	79	92.9	118	98	83.0	19	2	10.5
<i>Avena sterilis</i> L.....													
Burt.....	175	43	0	0	50	0	0	67	0	0	—	—	—
Fulghum.....	129	35	0	0	85	0	0	97	1	1.0	50	0	0
Navarro.....	946	—	—	—	—	—	—	12	0	0	—	—	—
Red Rustproof.....	131	52	0	0	86	0	0	98	0	0	28	0	0
<i>Avena strigosa</i> Schreb.....	587	56	0	0	103	0	0	95	0	0	46	0	0

Race IX is based upon Collection No. 12, which was obtained from Dr. L. R. Hesler, University of Tennessee, Knoxville, Tennessee, in the summer of 1924. The special feature of this collection is its capacity to infect the Fulghum oats of the *Sterilis* Group. Seven different strains of these oats, including Frazier and Kanota, have been tested in two or more experiments. The percentage of infection has varied from 62.5 to 82.7, and in some of the individual experiments, 100 per cent infection was obtained. It is evident that these oats are highly susceptible to this collection of smut.

On the other hand, the Red Rustproof type of *Avena sterilis* has proved to be entirely resistant. Six different strains, including Nortex, have been inoculated, and none of them has shown any infection. The varieties Burt, Nigra, and Selection, all recognized varieties of the Red Oat Group, have also proved to be negative to this collection.

The Hull-less oats, however, have proved to be susceptible, one strain giving 89.9 per cent infection. Liberty was tested in only one experiment, and gave a comparatively low number of infected plants. Orientalis (Seed No. 246) proved to be extremely resistant.

Among the *Sativa* types several, including Bicknell, Black Diamond, Canadian, Trisperma, Victor, and Winter Turf, gave high percentages of infection, and thus every indication of extreme susceptibility to this race. The variety Monarch gave 22 infected plants out of a total of 129 (17 per cent). Various other varieties, including Black Mesdag, Early Gothland, Green Russian, Joannette, Markton, Nebraska No. 21, Rosman, and Scottish Chief, proved highly resistant. No infected plants were obtained with *Avena strigosa* or *A. brevis*. On the other hand, *A. barbata* gave 100 per cent infection.

Two other collections have given results very similar to those just described. Collection No. 13 was obtained from Mr. T. R. Stanton, Office of Cereal Crops and Diseases, U. S. Department of Agriculture, who collected the smut on Fulghum oats at Lawton, Oklahoma, in June 1925; Collection No. 14 was obtained from Mr. P. B. Dunkle, Superintendent of Sub-Station No. 6, Texas Agricultural Experiment Station, Denton, Texas, also being collected on the variety Fulghum, in June 1925. In general, these two collections have given results corresponding with those obtained with No. 12. However, two or three differences stand out. While practically negative results were obtained with Collection No. 12 on *A. orientalis* (Seed No. 246), with Collection No. 13, 21 out of 45 plants (46.6 per cent) were infected, and with Collection No. 14, 11 out of 42 plants (26.1 per cent). Early Gothland gave negative results with No. 12, 96 plants being inoculated, and with No. 13, 29 plants out of 78 (37.1 per cent) were found infected, and with No. 14, 28 plants out of 72 (38.8 per cent). These results suggest the possibility of further specialization in these collec-

tions, although they all have the common capacity for attacking severely the Fulghum strains of Red oats.

Race X is based upon Collection No. 15. The original material was received from Mr. Dunkle in June 1925. It was collected on the Red Rustproof variety. Early experiments showed that

TABLE 5
Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED NO.	Avenae NO. 12 Tennessee			Avenae NO. 13 Oklahoma			Avenae NO. 14 Texas			Avenae NO. 15 Texas		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
<i>Avena barbata</i> Brot.....	830	16	16	100.0	15	15	100.0	18	18	100.0	16	12	75.0
<i>Avena brevis</i> Roth.....	289	43	0	0	38	0	0	29	0	0	18	0	0
<i>Avena nuda</i> L.....													
Hull-less.....	30	109	98	89.9	83	46	55.4	94	56	58.5	59	0	0
Liberty.....	292	18	3	16.6	19	4	21.0	19	7	36.8	20	0	0
<i>Avena orientalis</i> Schreb..	246	59	1	1.6	45	21	46.6	42	11	26.1	37	0	0
<i>Avena sativa</i> L.....													
Bicknell.....	341	38	34	89.4	39	12	30.7	37	31	83.7	15	1	6.6
Black Diamond.....	116	81	62	76.5	50	35	70.0	57	44	77.1	60	1	1.6
Black Mesdag.....	70	93	0	0	80	0	0	77	0	0	36	0	0
Canadian.....	119	84	80	95.2	55	50	90.9	58	44	75.8	58	49	84.4
Early Champion.....	150	—	—	—	—	—	—	—	—	—	18	0	0
Early Gothland.....	152	96	0	0	78	29	37.1	72	28	38.8	68	0	0
Green Russian.....	316	39	0	0	32	2	6.2	28	5	17.8	—	—	—
Joanette.....	187	20	0	0	19	0	0	18	0	0	20	0	0
Markton.....	752	35	0	0	37	0	0	34	0	0	42	0	0
Monarch.....	161	129	22	17.0	79	25	31.6	79	2	2.5	64	0	0
Nebraska No. 21.....	280	31	0	0	29	1	3.4	25	1	4.0	18	0	0
Rossman.....	322	30	0	0	28	3	10.7	30	1	3.3	—	—	—
Scottish Chief.....	124	72	2	2.7	58	6	10.3	50	3	6.0	38	0	0
Trisperma.....	64	27	16	59.2	25	2	8.0	26	8	30.7	17	0	0
Victor.....	126	94	75	79.7	58	27	46.5	56	30	53.5	35	2	5.7
Winter Turf.....	236	22	21	95.4	—	—	—	—	—	—	—	—	—
<i>Avena sterilis</i> L.....													
Burt.....	175	89	1	1.1	62	4	6.4	66	2	3.0	32	3	9.3
Frazier.....	914	39	27	69.2	58	19	32.7	59	36	61.0	58	0	0
Fulghum.....	129	120	75	62.5	118	79	66.9	122	90	73.7	60	0	0
".....	257	79	64	81.0	36	24	66.6	58	51	87.7	43	0	0
".....	696	91	61	67.0	43	35	81.3	45	39	86.6	20	0	0
".....	745	81	67	82.7	96	59	61.4	95	69	72.6	47	1	2.1
Kanota.....	264	89	71	79.7	82	48	58.5	81	68	83.8	15	0	0
".....	906	38	27	71.0	54	30	55.5	54	42	77.7	38	1	2.6
Navarro.....	946	19	0	0	32	0	0	37	0	0	33	0	0
Nigra.....	130	37	0	0	36	0	0	34	0	0	37	2	5.4
Nortex.....	907	37	0	0	55	0	0	57	0	0	51	25	49.0
Red Rustproof.....	131	101	0	0	83	0	0	86	0	0	81	52	64.1
".....	263	18	0	0	19	0	0	13	0	0	49	28	57.1
".....	265	85	0	0	69	1	1.4	70	0	0	150	91	60.6
".....	355	90	0	0	69	0	0	57	0	0	36	27	75.0
".....	746	87	0	0	88	0	0	83	0	0	69	39	56.5
Selection.....	132	35	0	0	31	0	0	35	0	0	32	0	0
<i>Avena strigosa</i> Schreb...	587	20	0	0	20	0	0	20	0	0	—	—	—

the original material was a mixture, but a very distinct race, capable of attacking Red Rustproof, was separated out. Five strains of this variety gave infections ranging from 56.5 to 75.0 per cent. Nortex, in three tests, gave 25 infected plants out of 51 (49.0 per cent). In striking contrast to these results,

the Fulghum strains gave negative results. Burt, Navarro, and Selection also proved to be essentially negative.

This race also proved incapable of infecting *Avena brevis*, *A. nuda* and *A. orientalis*. It was not tested on *A. strigosa*. Among the varieties of *A. sativa*, only one, Canadian, showed any conspicuous susceptibility to the race. With this variety, 49 out of 58 infected plants (84.4 per cent) have been obtained. *Avena barbata* has proved to be highly susceptible in the one experiment in which it was inoculated.

Race XI is based upon Collection No. 3. This was made by Dr. C. R. Hursh at Bandole, France, in May 1924, on *Avena barbata*. It has proved to be a very distinct specialized race of the loose smut, being capable of infecting only *A. barbata*, the host upon which it was collected. Practically negative results have been obtained with *A. brevis*, *A. nuda*, *A. strigosa*, *A. sterilis*, and six varieties of *A. sativa*, including Black Mesdag, Canadian, Early Gothland, Monarch, Scottish Chief, and Victor.

The evidence is clear that at least eleven distinct races of loose smut are found among the collections which have been used in these experiments. It is further probable that one or two other races may be differentiated. Further experiments, however, will be necessary in order to determine this.

The outstanding features of all of these races may be mentioned. *Avena barbata* is susceptible to all of them, although it has not been tested with Races II and III. Extremely high infections have been obtained with such diverse races as I and IX.

In contrast to *Avena barbata*, *A. brevis* has proved to be entirely resistant. It has been tested with all of the different races, and not a single plant has been found to be infected. Only one strain of *A. strigosa* has been used with these races, and it has proved essentially negative in every case except with Race I. It is possible, of course, that other strains or varieties of *A. brevis* and *A. strigosa* would show a susceptibility to one or more of these specialized types.

Avena orientalis (Seed No. 246) has proved to be highly susceptible to only Race I. It is somewhat susceptible to Collections No. 13 and 14, and this may be sufficient to separate these collections off from No. 12, which are now grouped as

Race IX. Green Mountain is very susceptible to Races I, II, III and IV, but has proved to be negative to V, VI, VII, and VIII, not having been tested with the remaining three.

Hull-less (Seed No. 30) is very susceptible to Races I, II, III, IV, V, and IX, being negative to all the others. Liberty

TABLE 6
Summary of results with *Ustilago levis* (K. & S.) Magn.^a

SPECIES AND VARIETY	SEED NO.	PHYSIOLOGIC RACE									
		I					II	III	IV	V	
		Missouri	Canada	Washington	Holland	Italy	Wales	France	England	China	
		COLLECTION NUMBER									
		1	7	8	9	4	6	3	5	10	
<i>Avena barbata</i> Brot.....	830	4	—	—	—	5	4	5	5	—	
<i>Avena brevis</i> Roth.....	289	1	2	2	2	2	5	1	2	0	
<i>Avena nuda</i> L.....											
Hull-less.....	30	5	5	5	5	5	1	0	2	4	
Liberty.....	292	5	5	5	5	5	—	0	0	4	
<i>Avena orientalis</i> Schreb.....	246	1	0	0	2	0	0	0	0	0	
Green Mountain.....	110	5	5	5	5	5	—	0	0	0	
<i>Avena sativa</i> L.....											
Bicknell.....	341	1	1	1	1	1	0	1	1	0	
Black Diamond.....	116	1	1	3	3	2	0	0	4	0	
Black Mesdag.....	70	0	0	0	0	0	0	0	0	0	
Black Norway.....	118	0	0	0	0	0	0	0	0	0	
Canadian.....	119	5	5	5	5	5	1	5	5	5	
Early Champion.....	150	5	5	5	5	5	0	0	0	0	
Early Gothland.....	152	1	1	0	0	0	0	1	1	0	
Green Russian.....	316	0	0	0	0	0	0	0	1	—	
Joanette.....	187	0	0	0	0	0	—	5	4	0	
Markton.....	752	1	0	0	0	1	0	0	0	0	
Monarch.....	161	5	5	5	5	5	0	5	5	0	
Monarch Selection.....	162	0	0	—	0	1	0	0	0	0	
Nebraska No. 21.....	280	0	1	0	1	0	0	0	0	0	
Rossman.....	322	0	0	1	0	2	0	0	0	—	
Scottish Chief.....	124	0	0	0	0	0	0	0	0	0	
Trispermia.....	64	0	0	0	0	0	0	0	1	0	
Victor.....	126	5	5	5	5	5	0	4	5	5	
<i>Avena sterilis</i> L.....											
Burt.....	175	2	1	1	2	1	0	0	1	1	
Fulghum.....	129	1	0	0	0	0	0	0	0	0	
Navarro.....	946	0	0	—	0	—	—	—	0	—	
Red Rustproof.....	131	1	0	0	0	0	0	0	0	0	
<i>Avena strigosa</i> Schreb.....	587	4	3	4	3	4	5	3	2	1	

^a In the body of this table numerals are used as symbols with the following significance:

—=No trial

2=11-25 per cent

5=75-100 per cent

0=No infection

3=26-50 per cent

1=1-10 per cent

4=51-75 per cent

oats usually corresponded very closely with this variety.

Among the varieties of *Avena sativa*, Black Mesdag and Markton were completely resistant to all of the races; no infections were obtained with either of them. Markton was not

used in the experiments with Race XI. The variety Canadian has proved to be extremely susceptible. It was attacked by all of the races except XI. It is further interesting that it is the only variety of this group which was infected by the Red Rustproof Race. Victor is almost as susceptible a variety as Canadian. Its susceptibility corresponded with this variety in every respect, except that it proved to be resistant to Race X as well as to Race XI. The other thirteen varieties grown varied greatly in their susceptibility to the different races, and on this account made possible the differentiation between the different collections.

The varieties of *Avena sterilis* have proved resistant to all the races except two. The Fulghum types are very susceptible to Race IX and the Red Rustproof types to Race X. These races are distinguished respectively by their capacity to infect Fulghum and Red Rustproof oats.

It is further interesting to note that Miss Sampson (1929) has described a specialized race of *Ustilago Avenae* which is capable of attacking *Avena brevis*. The material was collected on *A. strigosa*, and the race is especially characterized by its capacity for infecting the three subspecies of *A. strigosa*—*pilosa*, *orcadensis*, and *glabrescens*—as well as *A. brevis*. It has proved to be entirely negative on *A. nuda* and varieties of *A. sativa*.

PHYSIOLOGIC RACES OF USTILAGO LEVIS

Nine different collections of the covered smut obtained from different sources have been used in more or less extended experiments. Practically the same series of species and varieties of oats have been used as those employed in the different series with the loose smut. The data are recorded in tables 6 to 9.

The outstanding features of all the nine collections are as follows:

First. The high degree of susceptibility of *Avena barbata* to all the collections with which it was inoculated. Unfortunately, it was not included in the series with four of the collections of covered smut. In all the other cases, high percentages of infection, ranging from 72 to 100 per cent, have been obtained.

Second. *Avena brevis* has usually been infected to a slight degree, only one collection giving negative results. With

Collection No. 6 it has given almost 100 per cent of infected plants.

Third. *Avena orientalis* (Seed No. 246) has proved almost completely resistant to all of the collections, only one stray plant out of a total of 116, inoculated with Collection No. 1, being smutted; a few smutted plants were also obtained with collection No. 9. Green Mountain has given 100 per cent infection with several of the collections and negative results with the remainder.

Fourth. In the *Sativa* Group, many varieties stand out as sharply resistant: Black Mesdag, Black Norway, Early Gothland, Green Russian, Markton, Monarch Selection, Nebraska No. 21, Rossman, Scottish Chief, and Trisperma. In some of these varieties, notably Early Gothland, an occasional smutted plant has been observed, but usually all the plants in the experiments have remained free. The other varieties grown in the experiments have shown susceptibility to some of the collections, but resistance to the others.

Fifth. The varieties of *Avena sterilis* have, as a rule, shown a high degree of resistance. No collection of the covered smut has shown a marked capacity for attacking any variety of this species.

Sixth. Only one strain of *Avena strigosa* has been used in the experiments with all of the different collections; usually it has proved to be very susceptible, although one collection gave practically negative results.

On the basis of the behavior of the different collections on the varieties grown, especially Hull-less, Green Mountain, Bicknell, Black Diamond, Canadian, Early Champion, Joannette, Monarch, and Victor, at least five distinct races of the covered smut can be distinguished.

Race I is based upon Collection No. 1. The original material was collected near Columbia, Missouri, many years ago, and has been used in various experiments during the intervening years. Its outstanding features are its ability to severely infect Hull-less and Liberty, Green Mountain, Canadian, Early Champion, Monarch, and Victor. All of these have proved to be highly susceptible to this race of smut.

Avena brevis has generally given negative results, but occasionally partially smutted plants have been secured. These

are characterized by a marked dwarfing of the infected stalks as compared with the usual height of the normal.

The varieties Burt, Fulghum, and Red Rustproof have all shown a high degree of resistance. Occasionally an infected plant has been observed, particularly in the Burt and Fulghum varieties.

The strain of *Avena strigosa* has shown a high degree of susceptibility. Several other varieties belonging to the various

TABLE 7
Results with Ustilago levis (K. & S.) Magn.

SPECIES AND VARIETY	SEED NO.	Levis NO. 1 Missouri			Levis NO. 6 Wales			Levis NO. 10 China		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
<i>Avena barbata</i> Brot.....	830	36	26	72.2	23	17	73.9	—	—	—
<i>Avena brevis</i> Roth.....	289	103	9	8.7	112	109	97.3	35	0	0
<i>Avena nuda</i> L.....										
Hull-less.....	30	118	112	94.0	127	2	1.5	55	35	63.6
Liberty.....	292	20	20	100.0	—	—	—	21	12	57.1
<i>Avena orientalis</i> Schreb.....	246	116	1	0.8	51	0	0	36	0	0
Green Mountain.....	110	13	13	100.0	—	—	—	35	0	0
<i>Avena sativa</i> L.....										
Bicknell.....	341	83	4	4.8	32	0	0	16	0	0
Black Diamond.....	116	53	5	9.2	15	0	0	33	0	0
Black Mesdag.....	70	100	0	0	75	0	0	38	0	0
Black Norway.....	118	57	0	0	28	0	0	19	0	0
Canadian.....	119	125	125	100.0	98	5	5.1	18	18	100.0
Early Champion.....	150	43	41	95.3	20	0	0	37	0	0
Early Gothland.....	152	135	5	3.7	87	0	0	20	0	0
Green Russian.....	316	73	0	0	62	0	0	—	—	—
Joanette.....	187	93	0	0	—	—	—	39	0	0
Markton.....	752	45	2	4.4	39	0	0	32	0	0
Monarch.....	161	160	157	98.1	106	0	0	55	0	0
Monarch Selection.....	162	47	0	0	25	0	0	40	0	0
Nebraska No. 21.....	280	40	0	0	5	0	0	17	0	0
Rossman.....	322	65	0	0	20	0	0	—	—	—
Scottish Chief.....	124	110	0	0	81	0	0	37	0	0
Trisperma.....	64	69	0	0	37	0	0	15	0	0
Victor.....	126	139	136	97.8	122	0	0	39	32	82.0
<i>Avena sterilis</i> L.....										
Burt.....	175	52	6	11.5	44	0	0	29	2	6.8
Fulghum.....	129	86	4	4.6	64	0	0	20	0	0
Navarro.....	946	13	0	0	—	—	—	—	—	—
Red Rustproof.....	131	77	2	2.5	44	0	0	35	0	0
<i>Avena strigosa</i> Schreb.....	587	90	63	70.0	82	79	96.3	48	2	4.1

subspecies of *A. strigosa* have also proved to be very susceptible. Individual tests have been made with *pilosa*, *orcadensis*, and *glabrescens*. One strain, however, has given negative results.

Four other collections have given practically the same results as those obtained with Collection No. 1: No. 4 collected by Dr. C. R. Hursh near Bologna, Italy, in 1924; No. 7 by Prof. W. P. Fraser in Canada; No. 8 by Prof. George L.

Zundel at Pullman, Washington, and No. 9 by Dr. Theo. Roemer, who obtained it from Holland. These four collections from widely separated localities have run quite parallel to the original collection from Missouri. The varieties used in the present experiment have not been sufficient for showing any specialization of these collections, if such specialization actually exists.

Race II is based on material originally received from Miss Sampson in Wales in 1923, and data obtained from experiments with this collection have already been published. A second collection was received in 1925 from Dr. Pethybridge, who, however, obtained the material from Miss Sampson. The data presented in the table were secured with this collection, No. 6, but it has shown complete conformity with the original one received from Wales.

The conspicuous features of Race II are its capacity to infect *Avena brevis* and *A. strigosa*. Usually, 100 per cent of infected plants is obtained. It is equally severe on practically all varieties of *A. strigosa*, although one or two distinct strains have shown complete resistance; several strains of *A. brevis* have also proved to be entirely resistant. On the other hand, it is negative or nearly so on all varieties of *A. nuda*, *A. sativa*, *A. orientalis* and *A. sterilis*.

Race III is based upon Collection No. 3. The material was sent to me by Dr. C. R. Hursh from St. Cannot, France in 1924. The race shows a limited capacity for infecting oat varieties. It is entirely negative on the *Avena nuda*, *A. orientalis*, and *A. sterilis* groups, and only four varieties of *A. sativa* have proved to be susceptible, namely, Canadian, Joannette, Monarch, and Victor. It has not given very high percentages of infection of *A. strigosa*, and only a few partially infected plants of *A. brevis* have been obtained.

The outstanding features of the race, as compared with I, are its inability to infect Hull-less, Liberty, Green Mountain, and Early Champion. It is equally conspicuous by its capacity for infecting Joannette, a variety which has given negative results with Race I.

Race IV is based upon Collection No. 5, which was sent to me by Dr. Pethybridge from Shinfield, Berkshire, England. It shows a close similarity to Race III. It has almost the same

ability to infect the varieties. It is negative or practically so on the Hull-less oats, Green Mountain, and Early Champion. It severely infects such varieties as Canadian, Joannette, Monarch, and Victor. It is distinguished from the previous race by its ability to infect Black Diamond. With this variety, out of 52 plants inoculated, 38 (73.0 per cent) have been smutted. On the other hand, 50 inoculated plants with Race III gave entirely negative results.

TABLE 8
Results with Ustilago levis (K. & S.) Magn.

SPECIES AND VARIETIES	SEED NO.	Levis No. 7 Canada			Levis No. 8 Washington			Levis No. 9 Holland		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
<i>Avena barbata</i> Brot.	830	—	—	—	—	—	—	—	—	—
<i>Avena brevis</i> Roth.	289	68	11	16.1	47	9	19.1	72	9	12.4
<i>Avena nuda</i> L.	30	75	61	81.3	56	46	82.1	83	71	85.5
Hull-less.	292	19	17	89.4	20	17	85.0	20	19	95.0
Liberty.	246	43	0	0	52	0	0	51	6	11.7
<i>Avena orientalis</i> Schreb.	110	34	34	100.0	14	13	92.8	34	34	100.0
Green Mountain.	—	—	—	—	—	—	—	—	—	—
<i>Avena sativa</i> L.	341	37	1	2.7	30	1	3.3	38	3	7.8
Bicknell.	116	31	3	9.6	16	7	43.7	32	12	37.5
Black Diamond.	70	51	0	0	52	0	0	54	0	0
Black Mesdag.	118	19	0	0	17	0	0	17	0	0
Black Norway.	119	76	76	100.0	51	51	100.0	79	78	98.7
Canadian.	150	61	58	95.0	17	15	88.2	57	50	87.7
Early Champion.	152	61	1	1.6	52	0	0	60	0	0
Early Gothland.	316	15	0	0	10	0	0	15	0	0
Green Russian.	187	58	0	0	17	0	0	56	0	0
Joannette.	752	48	0	0	39	0	0	39	0	0
Markton.	161	120	113	94.1	54	54	100.0	119	110	92.4
Monarch.	162	19	0	0	—	—	—	20	0	0
Monarch Selection.	280	32	3	9.3	24	0	0	29	1	3.4
Nebraska No. 21.	322	15	0	0	14	1	7.1	15	0	0
Rossmann.	124	45	0	0	50	0	0	54	0	0
Scottish Chief.	64	20	0	0	19	0	0	27	0	0
Trisperma.	126	78	75	96.1	50	50	100.0	84	81	96.4
Victor.	—	—	—	—	—	—	—	—	—	—
<i>Avena sterilis</i> L.	175	41	4	9.7	36	3	8.3	46	8	17.3
Burt.	129	39	0	0	37	0	0	38	0	0
Fulghum.	946	12	0	0	—	—	—	11	0	0
Navarro.	131	18	0	0	18	0	0	23	0	0
Red Rustproof.	587	83	22	26.5	31	19	61.2	83	25	30.1
<i>Avena strigosa</i> Schreb.	—	—	—	—	—	—	—	—	—	—

Race V is based upon Collection No. 10. The original material came from the Experimental Farms at Sui-Yuan, Inner Mongolia, being sent to me by Prof. Chunjen C. Chen in 1927. The race stands out sharply by its ability to infect Hull-less and Liberty and also Canadian and Victor. It has proved to be negative or practically so to all the other varieties on which it has been tried. It is especially striking that it has failed to infect *Avena brevis*, *A. strigosa*, and such varieties of *A. sativa*

as Early Champion and Monarch. Unfortunately, it has not been used on *A. barbata*.

Miss Sampson (1929) has recently described a distinct new race of covered smut. She obtained a collection from England which proved capable of infecting severely certain varieties of *Avena sativa*, but was entirely negative on *A. strigosa orcadensis*, *A. brevis*, and practically so on *A. nuda*. It is evidently very close in its behavior to my Race IV.

TABLE 9

Results with Ustilago levis (K. & S.) Magn.

SPECIES AND VARIETY	SEED NO.	<i>Levis</i> NO. 4 Italy			<i>Levis</i> NO. 3 France			<i>Levis</i> NO. 5 England		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
<i>Avena barbata</i> Brot.....	830	12	12	100.0	13	13	100.0	18	18	100.0
<i>Avena brevis</i> Roth.....	289	114	15	13.1	122	8	6.5	115	13	11.3
<i>Avena nuda</i> L.....										
Hull-less.....	30	112	106	94.6	139	0	0	127	20	15.7
Liberty.....	292	17	15	88.8	18	0	0	17	0	0
<i>Avena orientalis</i> Schreb.....	246	52	0	0	75	0	0	60	0	0
Green Mountain.....	110	34	34	100.0	39	0	0	37	0	0
<i>Avena sativa</i> L.....										
Bicknell.....	341	29	2	6.8	25	1	4.0	27	1	3.7
Black Diamond.....	116	34	5	14.7	50	0	0	52	38	73.0
Black Mesdag.....	70	73	0	0	88	0	0	88	0	0
Black Norway.....	118	36	0	0	41	0	0	44	0	0
Canadian.....	119	97	97	100.0	106	105	99.0	145	138	95.1
Early Champion.....	150	36	34	94.4	38	0	0	62	0	0
Early Gothland.....	152	87	0	0	106	1	0.9	102	1	0.9
Green Russian.....	316	33	0	0	56	0	0	51	1	1.9
Joanette.....	187	37	0	0	36	31	86.1	55	29	50.9
Markton.....	752	50	2	4.0	45	0	0	37	0	0
Monarch.....	161	123	119	96.7	136	125	91.9	195	162	83.0
Monarch Selection.....	162	43	1	2.3	40	0	0	45	0	0
Nebraska No. 21.....	280	27	0	0	27	0	0	14	0	0
Rossman.....	322	19	2	10.5	20	0	0	15	0	0
Scottish Chief.....	124	68	0	0	99	0	0	84	0	0
Trisperma.....	64	50	0	0	50	0	0	44	1	2.2
Victor.....	126	90	88	97.7	120	77	64.1	148	125	84.4
<i>Avena sterilis</i> L.....										
Burt.....	175	38	3	7.8	56	0	0	86	2	2.3
Fulghum.....	129	59	0	0	75	0	0	72	0	0
Navarro.....	946	—	—	—	—	—	—	10	0	0
Red Rustproof.....	131	28	0	0	34	0	0	39	0	0
<i>Avena strigosa</i> Schreb.....	587	105	70	66.6	109	32	29.3	122	20	16.3

DISCUSSION

In the present experiments, fifteen different collections of *Ustilago Avenae* and nine of *U. levis* from widely separated localities have been studied with reference to their behavior on twenty-eight varieties and strains of oats belonging to seven different species. As a result of these experiments, eleven specialized races of loose smut and five races of covered smut have been differentiated on the basis of their capacity for infecting the varieties of oats grown.

So far as tested, all of the collections have proved capable of infecting *Avena barbata*. This species has been particularly susceptible to all races with which it has been inoculated. It is especially interesting that one race of *Ustilago Avenae* is distinguished by the fact that it is capable of attacking only this species.

None of the races of loose smut have shown any capacity for attacking *Avena brevis*. On the other hand, all the races of covered smut are capable of infecting this species, with the exception of Race V. However, only one race, II, has been able to produce a severe infection on this oat. In the other cases, relatively few plants have been smutted, and these only partially so.

Only two varieties of *Avena sativa*, Black Mesdag and Markton, have shown a conspicuous resistance to all races of both loose and covered smut. On the other hand, the varieties Canadian and Victor have shown unusual susceptibility to the various races of both species of smut. There are, however, two or three races to which these varieties have proved to be resistant.

The other varieties of *Avena sativa*, together with those of *A. nuda*, *A. orientalis*, *A. sterilis*, and *A. strigosa*, have shown varying degrees of susceptibility to the races of loose and covered smut, and it is through their behavior that the different races have been differentiated. It is particularly noteworthy that Black Norway, Early Gothland, Green Russian, Nebraska No. 21, Rossman, Scottish Chief, and Trisperma are unusually resistant to all races of covered smut, while extremely susceptible to one or more distinct races of loose smut. On the other hand, Monarch, and to some extent, Joannette, have proved more susceptible to the covered smut races.

It is interesting to note that there are sharply defined races of loose smut capable of attacking varieties of *Avena sterilis*, one being peculiar in its capacity for infecting Fulghum and another for infecting Red Rustproof. Further, I have found no well defined race of *Ustilago levis* which severely attacks any variety of this species. An occasional infected plant with some races of covered smut is observed, but so far, no distinct race of this smut, more or less restricted to these varieties, has been discovered.

It must be emphasized that the data obtained are based upon the use of well defined strains of oats. Other selections passing under similar names may give entirely different results; for example, certain varieties and strains of both *Avena strigosa* and *A. brevis* differ strikingly from those used. Further, I have a selection of Monarch which is exactly the reverse in its behavior to the one which I have grown in these experiments. It is negative to Race I of the covered smut, while highly susceptible to Race I of the loose smut.

It is obvious that these specialized races have special significance in the problem of the study of inheritance of smut resistance. It is just as important, in such investigations, to use known races of smut as it is pure line material of the oat varieties.

BROOKLYN BOTANIC GARDEN
BROOKLYN, N. Y.

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A morphologic study of the variations in *Stellaria aquatica* with special reference to symmetry and sterility

EDWIN B. MATZKE

(WITH THIRTY-TWO TEXT FIGURES)

The variability within the genus *Stellaria*, and even within certain species of that genus, has long been known and strongly emphasized; the coherence or trends within the genus and species, however, are by no means agreed upon, though the flowers form a very wide-ranging and possibly evolutionary series.

In the present study particular attention has been paid to *Stellaria aquatica* (L.) Scop. and *Stellaria media* (L.) Cyr., not with a view to distinguishing new varieties, but rather with the aim of determining the biological type for each of these species, which vary strikingly, not merely in different individuals, but, especially in *S. media*, in different parts of the same plant. The present paper gives the data on *S. aquatica*, and is to be followed by a study of the floral types in *S. media*, and of the correlation of external and internal variations in the flowers of these two species.

S. aquatica represents the maximum development, particularly as regards the number of parts in the flower, not only for the members of the genus, but for the Caryophyllaceae in general; and from such a type the increasing reduction in the number of parts in the flower of the Alsinoideae may well have progressed.

LITERATURE REVIEW

Linnaeus (in the *Species Plantarum*, 1753), classifying plants on the basis of the number of stamens and carpels, recognized the genera *Alsine* (p. 272), in which he included *A. media*, with five stamens and three carpels; *Stellaria* (p. 421) with ten stamens and three carpels; and *Cerastium* (p. 437) with ten stamens and five carpels. Because of its ten stamens and five carpels he placed the species now recognized as *Stellaria aquatica* in the genus *Cerastium*. Thus began the confusion in the nomenclature of the genus *Stellaria* which has resulted in the following extensive list of the more important synonyms of this species.

- Cerastium aquaticum* Linnaeus, Species Plantarum 439. 1753.
Stellaria aquatica Scopoli, Flora Carniolica ed. 2. 1: 319. 1772.
Alsine uliginosa Villars, Prospectus . . . Dauphin. 48. 1779.
Cerastium maximum Gilibert, Flora Lithuanica 2: 158. 1781.
Myosoton aquaticum Moench, Methodus plantas describendi 225. 1794.
Myosanthus aquaticus Desvauz, Jour. de Bot. Desv. II. 3: 227. [1816?]. (See note on page 531.)
Malachia aquatica Fries, Flora Hallandica 77. 1817.
Larbrea aquatica Seringe in DeCandolle, Prodromus Syst. Nat. 395. 1824.
Not *L. aquatica* A. St. Hilaire, Mém. Mus. Hist. Nat. 2: 287. 1815.
[=*Stellaria uliginosa* Murray, Prodr. Stirp. Gott. 55. 1770].
Cerastium deflexum DeCandolle, Prodromus Syst. Nat. 417. 1824.
Malachium aquaticum Fries, Novitiae Florae Suecicae 121-122. 1828;
Hegi, Illustrierte Flora Mittel-Europa 3: 348. 1911-1913.
Stellaria pentagyna Gaudin, Flora Helvetica 3: 179. 1828.
Stellaria media α *aquatica* O. Kuntze, Revisio Gen. Plant. 1: 52-55. 1891.
Alsine aquatica Britton, Mem. Torrey Club 5: 356. 1894; Small, Flora S. E. United States 421-423. 1913; Rydberg, Flora Rocky Mountains 268-271. 1917.

It is interesting to observe that the first change from the Linnaean disposition of the species was in its transference by Scopoli in 1772 from *Cerastium* to *Stellaria*, a position which would doubtless be regarded by a majority of modern taxonomists as expressing its natural affinity, and which appears to be confirmed by the present investigation. It will be seen, however, from the list, that opinion has varied widely in regard to the disposition of *S. aquatica*, from the attempts to constitute a separate genus for it on the one hand, to Kuntze's reduction of it to a mere variety of *S. media* on the other. The generic name *Malachium* Fries had rather wide acceptance in the literature of continental Europe during the nineteenth century (and even down to Hegi's recent *Flora*), though *Myosoton* Moench clearly has priority. Britton, finally, has revived the ancient genus *Alsine* (based according to him on the type species *A. media* L.), and restored to it the species separated under *Stellaria* by Linnaeus; in this he has been followed by Small, Rydberg, and some other American authors.¹ In Europe the

¹ Further confusion in regard to the use of *Alsine* has been introduced by the fact that House, in his *Annotated list of the ferns and flowering plants of New York State* (N. Y. State Mus. Bull. 254: 321-322), has interpreted the Linnaean genus *Alsine* as synonymous with *Spergularia* Pers. and *Tissa* and *Buda* Adans., while with Pax (1889) in Engler and Prantl, and other European authors the genus *Alsine* Wahlenb. has been in use for an entirely different group of species.

name *Stellaria* has been largely retained (Pax, 1889, in Engler and Prantl; Index Kewensis, 1895; Richter, 1897; Béguinot, 1910; Engler and Gilg, Syllabus der Pflanzenfamilien, ed. 9-10, 1924). *Stellaria* is used also in Gray's *New Manual of Botany*, ed. 7, and by some other American botanists.

When the species *S. aquatica* is included in the genus *Stellaria*, the more primitive character of its pistil is commonly emphasized by making it the sole species in a section of the genus, as in the section *Malachium* of Hooker (*Flora British India* 1: 229-230. 1875), or the subgenus *Myosoton* of Pax (1889).

A number of varieties of *S. aquatica* have been described. Lejeune² in addition to *Cerastium aquaticum* described *C. scandens*, which he said differed from the former by its twining habit. Fries³ mentioned a variety, *Malachium aquaticum* β *saxatile* with the stems four-angled, the leaves narrower than in the typical form, and the peduncles few and terminal. Fries recognized the possible influence of environment in this case, and added in a note that this form growing among the rocks of a canal would be exposed to heat and strong light. In his general description of *S. aquatica* Petermann⁴ characterized it as having a stem smooth below, glandulose-pubescent above, and then distinguished two forms, the first with the stem pubescent, the second with the stem smooth, but with the 'corymb only glandulose-pubescent.' Willkomm⁵ noted a form which he designated *Malachium calycinum*, differing from the normal form in its single line of cauline hairs, shorter leaves, non-glandular pedicels and calyx, and especially in the short, included petals. Godron⁶ described two varieties for Lorraine, *M. aquaticum* α *scandens*, 6-8 dm., climbing, leaves of the floral stem all sessile; and *M. aquaticum* β *arenarium*, a smaller plant, 1-3 dm., less developed in all its parts, with the lower leaves of the fertile stems petioled, truncate at the base, and the inflorescence poorly developed. The variety β *arenarium* was found in sand. Schur⁷ described two varieties: *M. aquaticum* *a* *alpinum*, with stems prostrate, 2.3-3 dm. long, leaves and stem pubescent, the lower leaves petioled; and *M. aquaticum* *b* *angustatum* hav-

² Lejeune, Flore des environs de Spa 210-211. 1811. ³ Fries, Nov. Fl. Suec. 121-122. 1828. ⁴ Petermann, Flora Lipsiensis 330-331. 1838. ⁵ Willkomm, Spicilegium florae Hispanicae. Bot. Zeit. 5: 233-241. 1847. ⁶ Godron,

ing stems erect-ascending, hirsute but smooth above ('superne glabris') the leaves 2.5 cm. long, 12.5 mm. wide, and purple veined. In a later publication Schur⁸ described three additional varieties: *M. aquaticum arenosum glomeratum*, distinguished chiefly by the bushy, stiff, upright character of the plants, the leaves smooth or nearly so, and the flowers fascicled at the apex of the stem; this form was found in sandy places and along railroad tracks; *M. aquaticum silvaticum molle*, characterized by its soft, dark green, much branched habit, glandular hairy above, leaves sharply punctate with white spots; flowers somewhat smaller than in the normal form; and *M. aquaticum hungaricum*, having recurved styles, plants slightly hairy and glandular, leaves all stalked.

The stem and inflorescence of the Caryophyllaceae, in addition to the treatment afforded them in the manuals, are discussed in a general way by Eichler (1878), Pax (1889), and Warming (1904). For *Silene* these features were taken up by Godron (1847) and Rohrbach (1868). The branching and inflorescence of the Caryophyllaceae were described more critically in the older literature by Wydler (1843, 1844, 1847, 1851, 1859), and by Wichura (1844, 1846, 1847). Wydler (1859) gave the general characters of the branching in *S. media* and *S. aquatica*, and Béguinot (1920) in *S. media*. Wydler made a few errors which were pointed out by Wichura and which he later acknowledged. The results given below are in general agreement with theirs, though the point of approach is somewhat different.

The arrangement of the branches is of course intimately associated with the arrangement of the leaves on the stem; and the subject of phyllotaxis is by no means settled. For many years the Fibonacci series, emphasized by Schimper and by Braun (1835) and others has served for textbook treatment of the subject. The contact, pressure and displacement (or slipping) theory as the explanation of leaf relationships was put forth by Schwendener (1878, 1901) and supported among others by Weisse (1889). It was extended and modified by Van

Flore de Lorraine, ed. 2. 1: 126-127. 1857. ⁷ Schur, Enum. Plant. Transsilvaniae 115-116. 1866. ⁸ Schur, Verh. Naturf. Ver. Brünn 15: 142-143. 1877.

Iterson (1907). However in its original form this theory is not generally accepted. It has been severely criticized among others by Winkler (1901, 1903), who showed that in some plants at least the 'contact' theory is impossible, and by Church (1901a, b, 1902, 1904, 1920). Emphasizing the study of the shoot apex in phyllotaxis, Church refers the phyllotax-mechanism to 'an initial choice of curve systems, comparable with the isolation of equal-spaced lines of growth-potential'; furthermore every lateral primordium he conceives as originating as 'a centric disturbance in a centric growth system.' He strongly criticizes the validity of the exact fractional divergences expressed by the numbers of the Fibonacci series, especially at the primordial apex. Church's work has been extensive and has been emphasized by Jaeger (1917) and Crow (1928).

It is well known that in some of the lower plants, as in some of the mosses and liverworts, there is a close relationship between the growth of the apical cell and the arrangement and size of the leaves. Even there, however, disturbing influences such as apical torsion must be considered (Correns, 1899). But the literature on the course of the cell divisions in the Spermatophyta is by no means as illuminating. The researches of Hanstein (1868), Strasburger (1872), Schwendener (1879), Groom (1885), and Koch (1891) satisfactorily disproved the contention of a general occurrence of single apical cells in the shoots of the Spermatophyta advocated by Dingler (1882, 1886) and Korschelt (1884), and correlations between apical cell divisions and leaf arrangements established in the lower plants can thus not be directly extended to the seed plants (see also Schwendener, 1885). The rules of rectangular intersection and division into equal parts formulated by Sachs (1878, 1887) as applied to cell divisions are not very helpful in the study of the relationship between the growth of the shoot and leaf arrangement, and the correlation between cell divisions in the shoot apex and phyllotaxis is left unanswered.

According to the view advocated especially by Velenovský (1887, 1907) and Čelakovský (1901, 1902) the plant is composed of a number of units ('Glieder'). Each unit has been variously called a 'phyton' (Gaudichaud, 1841), 'anaphyton' or 'anaphytum' (Schultz-Schultzenstein, 1843, 1847), and 'filopodio'

(Delpino; 1883). According to this theory each limb or unit is derived from the preceding by lateral growth, and the terminal growing point of the stem is of secondary origin. This view is based especially on embryological and seedling evidence. According to Velenovský a unit (anaphyt) consists of an internode and the node next above it, whether that node has one, two or several leaves. Čelakovský maintains on the other hand that this is only true in certain stems, such as those of the grasses; there a 'Sprossglied' consists of an internode and the node with its leaf next above it. However in stems having the usual spiral or whorled arrangements, in which a leaf subtends merely a portion of the stem, an anaphyt consists of a sector of the stem between one leaf and the next which stands directly above it, and the upper of these two leaves. Thus in the spiral arrangement the stem is composed of a number of 'Stengelglieder' arranged side by side, but beginning and terminating at different levels. According to both of these views the opposite leaf arrangement is of secondary origin. Church too refers to it as an 'afterthought.'

The occurrence of antidromy in plants has long been known, having been repeatedly discussed by Wydler and Wichura. Macloskie (1895 a, b, c, 1896 a, b, c) thought at first that plants were essentially internally homodromic, but antidromic as regards different individuals of the same species; he gave a list of plants to illustrate this, and even suggested the possible genetic significance of this phenomenon. However he later found that the principle of homodromy within the individual, antidromy between different individuals was not constant, and concluded that the law of antidromy was more complex than he had at first anticipated.

The external similarity between the clockwise and counter-clockwise arrangement of leaves or branches on an axis and the spirals of the shells of gasteropods is rather suggestive. As shown by Crampton (1894), Holmes (1900), Conklin (1903), and others the dextral and sinistral spirals are correlated with a definite spiral cleavage pattern; no such relationship has been reported in the seed plants. The production of leaf primordia in a definite pattern on the stem apex is different in some respects at least from the continuous spirals of gasteropod

shells. The similarities in principle, especially from the mathematical point of view, between phyllotaxis and shell construction in some of the Foraminifera are discussed by Van Iterson (1907). He also points out certain differences: on the vegetative apex the new leaves are established on the inner side of the folioid system, while new chambers in the shells of the Foraminifera are laid down on the outside; the constant factors are different and there are other dissimilarities.

The variability within the flowers of the genus *Stellaria* has come to be almost proverbial; it is discussed or mentioned in many of the textbooks. Among the more detailed studies of the different kinds of flowers should be mentioned first the very extensive researches of Béguinot (1910, 1920, 1921) as well as those of Reinöhl (1903) and Burkill (1895). These have been concerned especially with *S. media*, which displays the greatest variability of any of the members of the genus. Béguinot studied many of the varieties of that species. *S. aquatica* has been investigated by Béguinot (1914), who found the styles varying in number from six to two, and Kuntze (1891) who also reported on the variations in the gynoeceum. Bentham (1861, 1862) found the styles in Indian specimens not infrequently reduced to three; interesting additional evidence is also offered by many of the descriptive floras, some of which are listed above.

In the mature flower of *S. aquatica* the stamens opposite the sepals appear to be inside of those opposite the petals. This arrangement is the reverse of that found in most flowers and has given rise to the disputed question of the real nature of obdiplostemony. This was debated in the older literature which is reviewed by Eichler (1875). Hofmeister (1868) considered the stamens opposite the sepals as the original whorl; those opposite the petals he considered to have developed later and become interpolated between the whorl of petals and sepal stamens. Eichler at first adopted the view previously advocated by A. St. Hilaire that the stamens opposite the petals are merely split off from the petals and hence are really part of that whorl, the stamens opposite the sepals being the true whorl. Lüders (1907) and Wettstein (1911), on the other hand, consider the petals in the Caryophyllaceae to have arisen from the sta-

minal whorl. Later, however, Eichler (1878) accepted the theory suggested by Payer (1857) and advocated especially by Čelakovský (1875) that the diplostemonous arrangement was the original one, but that by displacement ('Verschiebung') the whorls became reversed as to position. This view is also accepted by Velenovský (1910). However, Čelakovský (1894) later abandoned this view and considered the obdiplostemonous arrangement associated with reduction. Schumann (1889) pointed out that obdiplostemony may be found in flowers in which the stamens opposite the sepals are the first to develop, and in others in which those opposite the petals develop first; he suggested contact as an explanation of the position of the carpels with reference to the two staminal whorls.

Payer (1857) figured the stages in the development of the flower of *S. aquatica*, and as shown in his figures 6 and 7, plate 73, the first stamens arise alternating with the petals. In figures 10 and 17, plate 73, he drew the sepal stamens higher up on the axis than the petal stamens. Schumann (1889) stated that in *Melandrium* and *Lychnis* the episepalous stamens originate first and lower down on the axis. *Malachium aquaticum*, he reported, differs in that the epipetalous stamens are inserted deeper than in *Melandrium*, but he was unable to determine whether or not the two whorls were inserted at the same level. Rendle (1925) states that the antesepalous stamens in the Caryophyllaceae not only arise before the antepetalous, but that their vascular strands in the floral axis stand outside of those leading to the antepetalous stamens, and that the obdiplostemony is therefore only apparent.

It may be worth while, furthermore, to call attention to the fact that, although in most families characterized by obdiplostemony (e.g. Crassulaceae, Geraniaceae, Onagraceae, and Ericaceae) the phenomenon finds complete expression, that is, in association with the reversed position of the two stamen whorls the carpels also are placed opposite the petals (rather than opposite the sepals), in the Caryophyllaceae, on the other hand, as shown by Eichler, two degrees of obdiplostemony are exhibited: an incomplete obdiplostemony in *Cerastium* (as also in *Lychnis* and *Viscaria* of the Silenoideae, cf. Eichler's diagram, 1875, p. 106), where only the two whorls of anthers

show the reversed position, the carpels still being opposite the sepals; and apparently complete obdiplostemony in *Stellaria aquatica* (as also in *Spergula arvensis* L.), where the carpels are opposite the petals.⁹ *Cerastium*, then, may be regarded as the most primitive genus we have in the Alsinoideae.

Both the stamens and pistils of *S. aquatica* show sterility to some extent. In the case of the androecium at least, in plants growing wild, this is a seasonal and hence in a measure a cyclic phenomenon. Sterilities associated with the partial or complete abortion of one or the other or both kinds of sporophylls are rather general in the Spermatophyta. Thus for example Stout (1922) found flower abortion at the beginning of the flowering period in *Brassica pekinensis* and *Brassica chinensis*, and arrested development of the flowers at the end; in addition he found other classes of sterility in the intervening period. The modification of one or more of the stamens into staminodia in the Caryophyllaceae was discussed by Darwin (1868, 1877). It is treated further by Henslow (1888) and Rendle (1925), both of whom contend that low temperature is the cause.

Among the classifications of sterility may be mentioned that of Stout (1916) in which he distinguishes three main groups: sterility from impotence, sterility from incompatibility, and embryo abortion. In the first of these, which includes the kinds of sterilities described below for *S. aquatica*, Stout mentions complete impotence involving either the absence of all floral and sex organs, or the lack of sporophylls only, and partial or com-

⁹ This difference of carpel position seems to furnish a more fundamental basis for the separation of the genera *Cerastium* and *Stellaria* than that usually given in our current manuals, viz. the form and dehiscence of the capsule. It is surprising that this difference has been overlooked by the authors of 'Gray's New Manual of Botany', 7th Edition, for in spite of their general adherence to the taxonomic arrangement of Pax (1889), who treated this point correctly, they have made the erroneous and misleading statement in both key and generic diagnosis that the styles of *Stellaria* are opposite the sepals. That not only styles (as shown in the figures illustrating this paper) but also the entire carpels are opposite the petals may easily be demonstrated in transverse sections of young flower buds, where the ovary shows complete septa opposite the sepals, which break down to produce the 'free central placenta' of the mature pistil. Even when the carpels are reduced to three (as in *S. media*, cf. Eichler's fig. 41, F) two of them are essentially opposite petals.

—T. E. H.

plete impotence with reference to one or the other or both types of sporophylls. Sirks (1917) distinguishes two main classes of sterility: sterility of the gametes, and sterility of the zygotes; the former he subdivided into partial unilateral, partial bilateral, total unilateral and total bilateral sterility of the gametes. The sterilities in *S. aquatica* discussed below can also be relegated to these different categories.

DISCUSSION OF SYSTEMATIC LITERATURE AND DESCRIPTION

Whether the different forms of *S. aquatica* which have been described, that amount to different varieties, will stand the test of being grown and propagated from seed is very problematical indeed. Whether the twining habit is a characteristic peculiar to one or more varieties, or whether it depends upon the presence and character of other neighboring plants has not been investigated. The stems of *S. aquatica* are usually more or less four-angled, and Fries was aware of the possibility of environmental influences in the characteristics of the variety *β saxatile*. Petermann's distinction, one variety having only the 'corymb' glandulose-pubescent, the other having the upper part of the stem pubescent as well, also needs further investigation. In the plants found in the vicinity of the city of New York it is not unusual to have just a single internode, directly below the inflorescence, glandulose-pubescent; in other cases several internodes just below the inflorescence are glandulose-pubescent. If Petermann had a form constantly glabrous up to the first flowering node it would certainly deserve to be ranked as a distinct variety; on the other hand in a fluctuating character like this, extended study is necessary before forms differing in the extent of pubescence can be admitted as good varieties. Ricker (1916) showed that the leaves of *Castanea mollissima* when exposed to strong light are densely pubescent with stellate and jointed hairs, while shaded leaves on the same tree are practically glabrous, all intergradations between these two types existing on the same individual. On the other hand the extensive researches of Béguinot (1907, 1910, 1920, 1921) on *Stellaria media* indicate that the extent of hairiness is a feasible line of approach to the separation of new varieties. Willkomm's description also suggests that he was dealing with a distinct variety. However the lowest pubescent internode not

uncommonly has just a sparse line of hairs, instead of being hairy throughout; sometimes this single line of hairs only extends part way down the internode. As for the short petals, it is not at all unusual for plants of *S. aquatica* to have some flowers with the petals equal to or shorter than the calyx, and in the colder weather of November the majority of the flowers in the vicinity of the city of New York are of this character. Willkomm's observations were apparently based on a limited amount of herbarium material, so much so that he was unable to report on the character of the lower leaves and the roots; here again, although the description is very suggestive, further research, especially on living growing plants, is necessary before the variety can be considered established. The two varieties of Godron may well be distinct. But the size of the plants is beyond doubt partly subject to the environment; and the plants, rooting at the nodes and dying off in the older parts may lose many of their stalked leaves. The two varieties of Godron are apparently different and should be further sought and studied. Of Schur's forms, the *M. aquaticum a alpinum* is similar to the *M. aquaticum β arenarium* of Godron. The form *M. aquaticum b angustatum* of Schur, with its purple veins and stem hirsute, smooth above—just the reverse of the condition usually obtaining—is striking indeed; the white punctate character of the leaves of the variety *M. aquaticum silvaticum molle* is very unusual; and the 'zurückgerollte Griffel' of the variety *M. aquaticum hungaricum*, in flowers that have been open for some time are the normal thing; if the styles are recurved when the flowers first open it is a noteworthy departure. The conclusive establishment of these different varieties awaits, then, the further study of their distinguishing characteristics in living, growing material.

Because of the unsettled state of this literature at present a description of the plants discussed below is here offered:

Stellaria aquatica (L.) Scop. Perennial. Roots fine, much branched. Stems ascending, spreading, partly decumbent or nearly erect, especially among other vegetation, 2.3 dm. to 10 dm. in length, more or less four-sided, glabrous below, pubescent and glandular-pubescent above. Leaves decussate, the lower ones petioled, the upper sessile; petioles ciliate, the longest

equal or subequal to the blade, shortening more or less gradually toward the apex of the stem. Lower leaves small, the blades about 1.3 cm. long, sometimes nearly as wide, sometimes longer; upper leaves often 5 cm.—6.3 cm. long, sessile or nearly so, ovate to ovate-lanceolate or oblong-ovate, the base tapering, truncate, rounded or cordate, the apex attenuate, acuminate or acute, the margin often undulate. Leaves (or bracts) of the inflorescence becoming smaller towards the ends of the cyme, as large as the leaves just below at the base of the inflorescence; floral leaves (bracts) and sometimes those just below finely glandular-ciliate and sparingly glandular-pubescent, especially on the veins above and below. Inflorescence typically a dichotomous cyme, some of the branches and flowers sometimes failing to develop; branches of the inflorescence typically terete, glandular-pubescent, the internodes, as in the stem, varying greatly in length. Pedicels glandular-pubescent, reflexed after anthesis and in fruit, the first formed in an inflorescence typically the longest, frequently 3.2 cm. in length, more often less. Sepals glandular-pubescent, ovate to ovate-lanceolate, more or less obtuse, usually about 8 mm. in length in fruit or less, scarious-margined. Petals white, nearly half again as long as the sepals (sometimes more, sometimes less), deeply bifid, lobes oblong, narrow. Stamens usually 10, the 5 sepaline glandular at the base, usually about $2/3$ as long as the petals. Styles usually 5, alternate with the sepals; stigmas minutely papillose above, whitish, erect at first, becoming reflexed (with the styles). Capsule ovoid-oblong to ovoid-lanceolate, usually somewhat longer than the sepals, splitting into 5 valves which are often bidentate. Seeds reniform, somewhat flattened, tuberculate.¹⁰

The essential differences between *S. aquatica* and *S. media* (and other members of the genus also) are very few, while the similarities are striking. In habit the two species are very close; the character and branching of the stems, the shapes of

¹⁰ Material and seed for this study were obtained from wild plants growing along the Bronx River in the New York Botanical Garden. Possibly these plants had "escaped" from a bed in the Garden. Plants for study have also been obtained from the vicinity of Ridgewood, New Jersey. *S. aquatica* is described in our manuals as 'adventive from Europe,' occasional in the eastern states. That it may be of relatively recent introduction might be inferred from the fact that it is not listed in Gray's *Manual*, 6th edition (1889). Taylor in his *Flora of the vicinity of New York* (Mem. N. Y. Bot Gard. 5: 305. 1915), calls it "a rare and local weed known definitely only near Philadelphia and New York." House (N. Y. State Mus. Bull. 254: 314. 1924) states that it is 'infrequent, but reported from many localities across the State.'

the leaves, the character of the pubescence, especially on the pedicels and calyx, the shape of the sepals and petals, the character of the stigmas, the markings on the seeds—all these are similar in their details in *S. aquatica* and *S. media*, especially the larger varieties of *S. media*. The most obvious differences between *S. aquatica* and the other members of the genus are in the number of the styles and the splitting of the capsules. *S. aquatica* usually has five styles, the other species usually three; but this difference is by no means constant, *S. media* sometimes having four styles, and *S. aquatica* not at all infrequently having that number. The other difference is in the splitting of the capsule, that of *S. aquatica* usually opening into five valves which are frequently two-toothed, while in the other members of the genus the capsule usually splits into six valves. These dissimilarities are sufficient to give *S. aquatica* species rank, but it seems hardly justifiable, in view of the many similarities between this and the other species, especially the larger varieties of *S. media*, to put it in a separate genus.

THE ROOT

A detailed study of the root system and root development is still to be made. However, a preliminary examination of the roots of often plants grown in pots shows that the primary root is comparatively well developed near the root collar. Near the surface of the soil large secondary roots are given off, the primary root decreases in size, and in three of the ten plants examined it was difficult to tell, about 1.6 cm. below the surface of the soil, which was the primary and which the secondary roots, since none was of outstanding diameter or growing straight down. In another instance it was easy to trace the course of the primary root as a well developed structure a little over 3 dm. long. The other six plants varied between these extremes. Some of the secondary roots were just as well developed as the primary root. All of these roots gave rise to a great mass of fine thread-like rootlets, and such structures may also develop from the nodes of the stem. These observations have not been very extended and await further and more searching investigation.



Fig. 1. Counterclockwise arrangement of the branches on the stem of *Stellaria aquatica*. Fig. 2. Clockwise arrangement of the branches on the stem of *S. aquatica*. ($\times 1/3$)



Fig. 3. Strongly and weakly developed branches each forming a counter-clockwise spiral on the same stem of *Stellaria aquatica*. Fig. 4. Reversal of the spiral formed by the branches on the stem of *S. aquatica*: the branch at the second node represented being clockwise to that at the lowest node, the succeeding ones all in counterclockwise spiral; young inflorescence also shown. ($\times 1/3$)

THE STEM AND INFLORESCENCE

With a view to determining the pattern, if any, in the arrangement of the branches, twenty plants raised from seed were watched and the progress of their growth recorded. The leaf arrangement is decussate. All the first formed leaves are petioled; it is only as the plants grow older that sessile leaves appear. The first node, or the first few nodes have as a rule two or more branches. Advancing up the stem of the young plants, however, a point is soon reached at which only one of the two leaves at a node bears a branch in its axil; and these branches originate in spiral fashion, one at each node, so that every fifth node will have a branch approximately above the first. It is obvious that this spiral arrangement can be of two kinds, clockwise as shown in figure 2, and counterclockwise as shown in figure 1. Of the twenty plants studied, eleven showed the clockwise arrangement of the primary branches on the main axis, and nine the counterclockwise.

Tables 1 and 2 show the arrangement of the branches on the lower portions of these twenty plants. The eleven plants in table 1 have the branches arranged in a clockwise spiral on the main stem, the nine in table 2 have the counterclockwise arrangement of the branches on the primary stem. A branch is usually formed in the axil of each of the leaves at the cotyledonary node. These branches have for the sake of convenience been numbered 1 and 2. Plant 12 thus had two branches, one in the axil of each leaf at this first node. The leaves are decussate, and therefore those at the second node are at right angles to those at the first node. The branch at the second node counterclockwise to branch number 1 at the first node has been arbitrarily designated 3; that in similar relation to number 2 has been called 4. This applies to plants in tables 1 and 2. All the other branches on the stem will originate above one of these four (making allowances for twisting of the stem). Thus in plant 12 there were two branches at the third node, one above each of those at the first node; that above number 1 is called 1', that above number 2 is called 2'. At the fourth node there was a single branch, that above number 3 and therefore designated 3'. Each node is probably potentially capable of producing a branch in the axil of each leaf. Thus at the fourth

node in plant 12 at some later time a branch number 4' might be produced; therefore the branch at the sixth node is not numbered 4' but 4". Not infrequently after a branch has arisen in the axil of a leaf a second branch will develop between the leaf and the first branch. In plant 1 for instance, in addition to branches number 1 and number 2 at the first node there were two others, that between number 1 and its leaf, which is designated 1a, and that between number 2 and its leaf, designated 2a. Each of the branches at a node will again have secondary branches in the axils of some of its leaves; and these secondary branches will also show a clockwise or counterclockwise arrangement on the primary branches. Thus in plant 12 there were two branches at the first node, and on one of these branches the smaller secondary branches were arranged in a counterclockwise spiral, on the other in a clockwise spiral. Therefore branch number 1 in plant 12 has been listed as counterclockwise, branch number 2 as clockwise. If the branch was present but too small to permit the determination of the arrangement of the smaller branches upon it that branch is indicated with a dash; if the arrangement was not clear it is indicated with a question mark; if no branch was present the space is left entirely blank. Some small branches on the main stem at nodes beyond those listed are not given in the tables.

It is evident from the tables that the several lowest nodes usually have a branch (or two branches) in the axil of both of the leaves. In plant 12 the first three nodes each had a branch in the axil of both of the leaves; the three succeeding nodes each had a single branch, and the smaller branches on these three were arranged counterclockwise, counterclockwise, and clockwise, respectively. Here the branches on plant 12 are given for only six nodes; in reality there were more, but they were too small to show the arrangement of the secondary branches upon them and hence are not listed. Of the twenty plants twelve had four branches at the first node, and all twenty had at least one branch in the axil of each leaf. This is of advantage to the plant in spreading over the surface of the soil since the lower branches grow at right angles or more or less opposite to the direction taken by the main stem.

In thirteen plants there was at least one branch in the axil of each leaf of the second node; ten had at least one branch in

TABLE 1
Arrangement of the secondary branches upon the primary branches of the main axis in Stelleria aquatica—the primary branches in each case being arranged in clockwise spiral upon the main axis^a

PLANT NUMBER	1	2	3	4	5	6	7	8	9	10	11	TOTAL cc	TOTAL c
Arrangement of the primary branches upon the main axis	c	c	c	c	c	c	c	c	c	c	c		
Arrangement of the secondary branches upon the primary branches of the first node	1 cc 1a c 2 cc 2a c	1 cc 1a cc 2 c 2a c	1 c 2 cc	1 c 2 cc?	1 c 1a c? 2 c 2a c	1 c 2 cc	1 c 2 c	1 c 1a cc? 2 c 2a cc	1 cc 1a c? 2 cc 2a cc	1 c 1a — 2 c 2a —	1 cc 2 cc	4 2 6 2	7 3 5 3
Arrangement of the secondary branches upon the primary branches of the second node	3 c 4 c 4a —	4 cc	3 cc 4 —	3 cc 4 c 4a —	3 c 4 c 4a —	3 c 4 c	3 cc 4 c	3 cc 4 c 4a —	3 c 4 c 4a —	3 cc 4 c	3 cc? 4 cc	6 2	4 7
Arrangement of the secondary branches upon the primary branches of the third node	2' c 2'a —	1' cc	1' c	2' c	1' cc? 2' cc	1' c 2' cc	2' cc	1' cc 2' c 2'a —	1' cc 2' c 2'a —	1' cc 2' c	2' cc	5 3	2 5
Arrangement of the secondary branches upon the primary branches of the fourth node	4' c 4'a —	3' — 4' c	4' cc	4' c	3' cc 3'a cc 4' c 4'a —	3' cc 3'a cc	3' cc 3'a —	3' c 3'a —	3' cc 3'a c	3' cc	3' c	4 1 1 1	2 1 1 4
Arrangement of the secondary branches upon the primary branches of the fifth node	2'' cc	2'' cc	2'' c	2'' c 2''a —	2'' c 2''a —	1'' cc 1''a —	1'' cc 1''a —	1'' cc 1''a —	1'' cc 1''a —	1'' c	1'' cc	5 2	1 3

TABLE 1 (continued)

PLANT NUMBER	1	2	3	4	5	6	7	8	9	10	11	
Arrangement of the secondary branches upon the primary branches of the sixth node	3'' c	3'' cc	3'' c 3'' _a —	3'' cc 4'' cc	3'' c 3'' _a —	4'' cc 4'' _a —	4'' cc	4'' cc	4'' cc		4'' cc	2 6 3
Arrangement of the secondary branches upon the primary branches of the seventh node	1''' c	1''' cc	1''' cc 1''' _a —	1''' cc	1''' c 1''' _a —	2''' c	2''' c	2''' c 2''' _a —	2''' cc 2''' _a —		2''' c	3 1 4 2
Arrangement of the secondary branches upon the primary branches of the eighth node		4''' cc		4''' cc	4''' —	3''' c	3''' cc	3''' cc 3''' _a —	3''' c 3''' _a —		3''' c	2 2 3 1
Arrangement of the secondary branches upon the primary branches of the ninth node		2''' cc		2''' cc			1''' c	1''' c	1''' cc 1''' _a —			1 2
Arrangement of the secondary branches upon the primary branches of the tenth node				3''' c			4''' cc	4''' cc	4''' cc			3 1
Arrangement of the secondary branches upon the primary branches of the eleventh node									2''' c 2''' _a —			65 64

^a In the columns of this table c=clockwise; cc=counterclockwise; a ? indicates a doubtful case; and a dash indicates that the branches were too undeveloped to permit determination of the direction of the spiral.

TABLE 2

Arrangement of the secondary branches upon the primary branches of the main axis in *Stellaria aquatica*—the primary branches in each case being arranged in counterclockwise spiral upon the main axis^a

PLANT NUMBER	12	13	14	15	16	17	18	19	20	TOTAL CC	TOTAL C	TOTAL CC	TOTAL C	TOTAL TABLES 1 AND 2 C	TOTAL C
Arrangement of the primary branches upon the main axis															
Arrangement of the secondary branches upon the primary branches of the first node	1 cc 2 c	1 c 1a cc 2 c 2a c	1 cc 1a cc 2 cc 2a —	1 cc 1a c 2 cc 2a cc	1 — 2 c	1 c 1a — 2 cc 2a —	1 cc 2 cc 2a —	1 cc 1a c 2 cc 2a c	1 c 1a — 2 cc 2a c	1 cc 1a — 2 cc 2a —	3 2 3 2	5 2 6 1	3 2 3 2	9 4 12 3	10 5 8 5
Arrangement of the secondary branches upon the primary branches of the second node	3 c 4 —	3 c 4 c	4 cc	3 c?	3 c	3 cc	3 c 4 c	3 cc 3a 4 cc 4a —			2 2	2 2	5 4	8 4	9 9
Arrangement of the secondary branches upon the primary branches of the third node	1' cc 2' c	1' c 2' cc 2'a —	1' c	1' c		1' — 2' cc?	1' cc 2' cc	1' cc 2' cc 2'a	1' c 2' c 2'a —		3 4 2	3 4	4 2	8 7	6 7
Arrangement of the secondary branches upon the primary branches of the fourth node	3' cc	3' c 3'a —	3' — 3'a —	3' c 3'a —	3' c 3'a — 4' cc?	3' cc 4' cc	4' c	4' cc 4'a	3' — 3'a 4' cc 4'a —		2 4 1	2 4	3 1	6 1 5	5 1 5
Arrangement of the secondary branches upon the primary branches of the fifth node	2'' cc	2'' c	2'' cc	2'' c 2'a	2'' cc	1'' cc?	1'' c	1'' cc 1'a	1'' c 1'a —		2 3	2 3	2 2	7 5	3 5

TABLE 2 (continued)

PLANT NUMBER	12	13	14	15	16	17	18	19	20		41	126	116
Arrangement of the secondary branches upon the primary branches of the sixth node	4'' c ?	4'' cc	4'' cc	4''' c 4'''a —		3'' cc	3'' c	3'' cc 3'''a —	3'' c 3'''a —	2	2	4	5
Arrangement of the secondary branches upon the primary branches of the seventh node		1''' cc	1''' —	1''' c		2''' cc	2''' cc	2''' cc 2'''a —	2''' cc	1	1	4	3
Arrangement of the secondary branches upon the primary branches of the eighth node		3''' cc	3''' c	3''' — 3'''a —			4''' cc	4''' cc 4'''a —	4''' c 4'''a —	1	1	3	4
Arrangement of the secondary branches upon the primary branches of the ninth node		2''' c	2''' cc	2''' cc 2'''a —			1''' c	1''' cc 1'''a —	1''' cc	2	1	4	3
Arrangement of the secondary branches upon the primary branches of the tenth node			4''' c ?								1	3	1
Arrangement of the secondary branches upon the primary branches of the eleventh node													1
										52	41	126	116

a In the columns of this table c=clockwise; cc=counterclockwise; a ? indicates a doubtful case; and a dash indicates that the branches were too undeveloped to permit determination of the direction of the spiral.

the axil of each leaf of the third node. At the fourth node however, only four plants had a branch on each side of the stem; at the fifth and sixth nodes none were so characterized. This indicates that there are often four branches at the first node and very frequently there is at least one in the axil of each leaf of the second and third nodes. It should be stated that these plants were grown during the unfavorable winter months, the final observations being made on May 21, when the plants were six months old but not particularly well developed. Field observation shows that six consecutive nodes on vigorously growing plants all with sessile leaves (indicating that they were some distance above the cotyledonary node) each had two branches. A somewhat similar condition is illustrated in figure 3. Only limited conclusions may be drawn from plants grown under the more or less artificial greenhouse conditions. Not all the branches develop at the same time or at the same rate, and further examination at a later date would have yielded further data.

A rather typical plant is number 13 in table 2; it has four branches at the first node, one branch in the axil of each leaf of the second node, one branch in the axil of one of the leaves of the third node and two in the axil of the other, and one branch at each of the succeeding nodes. Other plants show considerable variation from this. In plant 17 the second node has only a single branch, while the third and fourth have two each; in plant 20 the second node is devoid of branches, while there are three at the third and four at the fourth nodes.

In some cases the arrangement of the branches at least apparently changes from one direction to the other. Thus in plant 15 the branch at the third node, 1', is arranged clockwise with reference to branch number 3, but from there on the branches go up the stem in a counterclockwise spiral. Perhaps it should be stated again that "3'c" (in tables 1, 2) does not mean that branch number 3' is clockwise in its position with reference to the branch below (in this case it is counterclockwise); it means that the smaller secondary branches on branch number 3' are arranged in a clockwise spiral on that branch. Whether branch number 3' is clockwise or counterclockwise with reference to the branch at the node below is shown by the numbers assigned to the branches as described above. In plant 15 the apparent reversal

would be eliminated if there were two branches at the second node instead of one. Figure 4 shows a case similar to this. There the branch at the second node represented is clockwise to that at first, but from there on the branches are arranged in a counterclockwise spiral. Plant number 1 shows just the opposite condition; there branch number 4' is counterclockwise to branch number 2, but from there on the branches form a clockwise spiral. Here again there would be no reversal if there were a branch in the axil of each of the leaves of the third node, instead of the single branch there.

Branch number 2 of plant 11 had a secondary branch in the axil of each leaf of the first node, and each succeeding node had but a single branch; that at the third node was clockwise to that at the second, that at the fourth node clockwise to that at the third, that at the fifth node clockwise to that at the fourth; but the branch at the sixth node was counterclockwise to that at the fifth and those at the seventh, eighth, ninth, and tenth nodes formed a counterclockwise spiral. This would rather appear like a real reversal. As stated above, each node is probably potentially capable of producing at least one branch in the axil of each of the two leaves and when this occurs the branches are no longer arranged in a single spiral; but even if this occurred in a case like the one described above, they would then form two spirals (each with a reversal) in the order of their appearance; this would also be evident, as shown in figure 3, from the difference in size of the two branches at each node.

A record was also kept of the arrangement of the secondary branches on the primary branches (as in the case just described). In these primary branches each leaf of the first node, almost without exception, had a secondary branch in its axil and the succeeding nodes each had but a single branch, forming a clockwise or counterclockwise spiral as indicated in tables 1 and 2. The tertiary branches on the secondary were mostly in just the same fashion. Thus, while the main stem often had two or more branches at the first three nodes, the primary branches, in the earlier stages at least, usually had two secondary branches only at the first node; and the secondary branches, like the primary, usually had two tertiary branches only at the first node, and one at each node thereafter.

Irregularities were also found on the primary branches. Branch number 4 on plant 4 had a single branch in the axil of each leaf of the first node, but only a single branch at each succeeding node. But the branch at the third node was clockwise to that at the second; that at the fourth was clockwise to that at the third, that at the fifth counterclockwise to that at the fourth, that at the sixth counterclockwise to that at the fifth; the branch at the seventh node was clockwise to that at the sixth, and the succeeding ones all in a clockwise spiral. In this case, in which the branch exhibits two reversals in the spiral, if the branch at the fifth node were on the opposite side of the node, that is clockwise to the branch at the fourth node, the secondary branches would have formed a perfect clockwise spiral. Where there was a change in the direction of the spiral the final direction is the one given in the table.

Not infrequently two branches develop at a node, one in the axil of each leaf, while the nodes above and below have just a single one. Branch number 1 of plant 18 had the usual two branches at the first node, one at the second, third, and fourth nodes, two at the fifth, and one from there on; and the branch at the sixth node was correctly placed with reference to the others—that is the whole branch showed a counterclockwise arrangement of the smaller branches, with one extra branch, which does not enter into the spiral, at the fifth node. This additional branch, not merely here but in other cases as well, was less developed than that on the opposite side of the node. In some instances no branch developed at a node; as is to be expected the branch of the node above usually continues the spiral just as though the missing branch of the vacant node were present.

Sometimes there is a branch in the axil of each of the leaves of a node, with the single branch of the node above situated over the branch of the node below the one with the two branches. Or again there may be two branches, one above the other, with a single branchless node between.

A rather unusual case was found in the arrangement of tertiary branches on a secondary branch of plant 8. The first node had the usual two branches, the succeeding nodes just one. The branch at the third node was counterclockwise to that at the second, that at the fourth counterclockwise to that the third,

that at the fifth clockwise to that at the fourth, the branch at the sixth node counterclockwise to that at the fifth, and that at the seventh clockwise to that at the sixth. If the tertiary branches had originated in a counterclockwise spiral all the way-up this secondary branch, with the second, third, and fourth nodes just as they are, the branch of the seventh node would have had its present position, though those at the fifth and sixth would have been different. This branch showed three reversals in six nodes. While Thompson (1917) is undoubtedly correct in saying that phyllotaxy presents no 'subtle mystery' it would seem that cases like this do need further study to reveal their true nature. While it may well be true that each node is capable of producing a branch in the axil of each leaf, the question of why one develops more rapidly than the other must then be answered. When there are two branches at several consecutive nodes, the strongly and weakly developed branches often form two distinct spirals. This by no means exhausts the number or kinds of variations exhibited by the stem and its branches. However the aim is here rather to present the type and the common variations from that type. While the variations have been emphasized, they are really comparatively few.

Tables 1 and 2 show first the arrangement of the branches on the main stem. Of twenty plants there were nine that had these branches in a counterclockwise spiral, and eleven in a clockwise spiral. The nine plants of table 2, all having the primary branches in a counterclockwise spiral on the main stem, had a total of 93 primary branches which were developed well enough to disclose the arrangement of the secondary branches upon them; and of these 93 branches, 52 showed the counterclockwise and 41 the clockwise arrangement of the secondary branches upon the primary. Of these secondary branches 67 were developed far enough to show in turn the arrangement of the tertiary branches upon them—26 were in counterclockwise spiral, 41 in clockwise.

Table 1 shows the eleven plants of the twenty having the primary branches of the main axis arranged in a clockwise spiral. Of these primary branches, 129 were large enough to show how the secondary branches were arranged, and 65 had them in the counterclockwise spiral, 64 in the clockwise. On these eleven plants 75 secondary branches were sufficiently

developed to show the arrangement of the tertiary branches, and of these 35 indicated a counterclockwise, 40 a clockwise spiral. Adding all these together—the 20 main stems, the 222 primary branches, and the 142 secondary branches—187 showed the counterclockwise, 197 the clockwise spiral. Whether this difference is of any significance is very doubtful, though there is a positive correlation with the overlapping of the sepals of the first flower in the inflorescence as will be shown below.

Of the nine well developed branches of plant 17, eight showed the counterclockwise spiral of the secondary branches upon the primary, and only one the clockwise; on the other hand plant 5 had ten branches with the clockwise arrangement, and only one with the counterclockwise. Plants 6, 12, 18, and 20 each had an equal number of primary branches showing the clockwise and counterclockwise arrangement of their secondary branches. There seems to be no regularity in the arrangement of branches showing clockwise and counterclockwise spirals in the plant, though the total number of each in twenty plants was nearly the same.

The leaves of the younger plants are all petioled. Sometimes the leaves even at the base of the inflorescence are very short-petioled. This is unusual however; typically several pairs of leaves below the inflorescence are sessile. Sometimes a very considerable number of nodes, six or eight or more, have sessile leaves before the first flowering node is produced.

There is similar variation in the pubescence. For a distance of two internodes below the inflorescence the stems are as a rule glandular-pubescent. But this varies somewhat, sometimes three internodes, sometimes only one showing this distribution. The glandular character of the pubescence seems less pronounced some distance from the inflorescence. The stems are usually pubescent on all sides (where they are pubescent at all); but sometimes the pubescent internode farthest from the first flower has just a line of hairs, suggesting the condition in *Stellaria media*. The leaves (or bracts) of the inflorescence are glandular-pubescent as well as the branches, as are the leaves at the node below the first flower.

The flower of *S. aquatica* has five sepals, two outer, two inner and one partly outside and partly inside; this quincuncial imbrication is associated with the order of appearance of the

sepals in spiral sequence as described in the older literature (Wichura, 1847; Payer, 1857) and is typical for many dicotyledonous families. There are obviously two possible arrangements which are shown in figures 6 and 7; in these figures the sepals are numbered as in the works cited. When the main axis or one of the branches is terminated by a flower, the orientation of the critical sepal (number 3) is correlated with the clockwise or counterclockwise arrangement of the smaller branches upon the main axis or branch in question. When the arrangement of the branches is counterclockwise, the sepals are oriented as in figure 6 (clockwise); when it is clockwise, the sepals are oriented as in figure 7 (counterclockwise). This seems to hold with but very few exceptions. The first flowers on 153 branches were examined, and in 152 the overlapping of the sepals and the arrangement of the branches were as described above. In figures 6 and 7, *A* and *B* represent the bracts at the base of the pedicel of the flower, and *C* and *D* the bracts or leaves of the node below. Progressing up the stem in a counterclockwise spiral, the branch in figure 6 at the node below the one bearing the flower will be in the axil of the leaf *C*; progressing up the stem in a clockwise spiral, the similar branch in figure 7 will also be in the axil of the leaf *C*. Thus the position of the sepals with reference to the bracts, leaves, and branches is fixed. After anthesis the pedicel will bend, and it bends toward leaf *D* and away from leaf *C* in each case. A branch now appears in the axil of bracts *A* and *B*. This branch produces a single internode and then a node with two bracts, each with their midveins parallel to the midveins of bracts *C* and *D*. The branches bearing these bracts are not vertical like the stem, but oblique as in practically any dichotomous cyme. These points are shown in figure 4; the stem of the plant illustrated there was decumbent, becoming erect toward the apex; therefore in the drawing the inflorescence appears to project toward you. The branches in the axils of bracts *A* and *B* in figures 6 and 7 will be found each to produce a flower at the first node; this terminates each of these branches. But the flower of the branch in the axil of bract *A* in figure 6 will have the sepals originating in clockwise sequence as in figure 6; the flower terminating the branch in the axil of bract *B* in figure 6 will have the sepals originating in counterclockwise

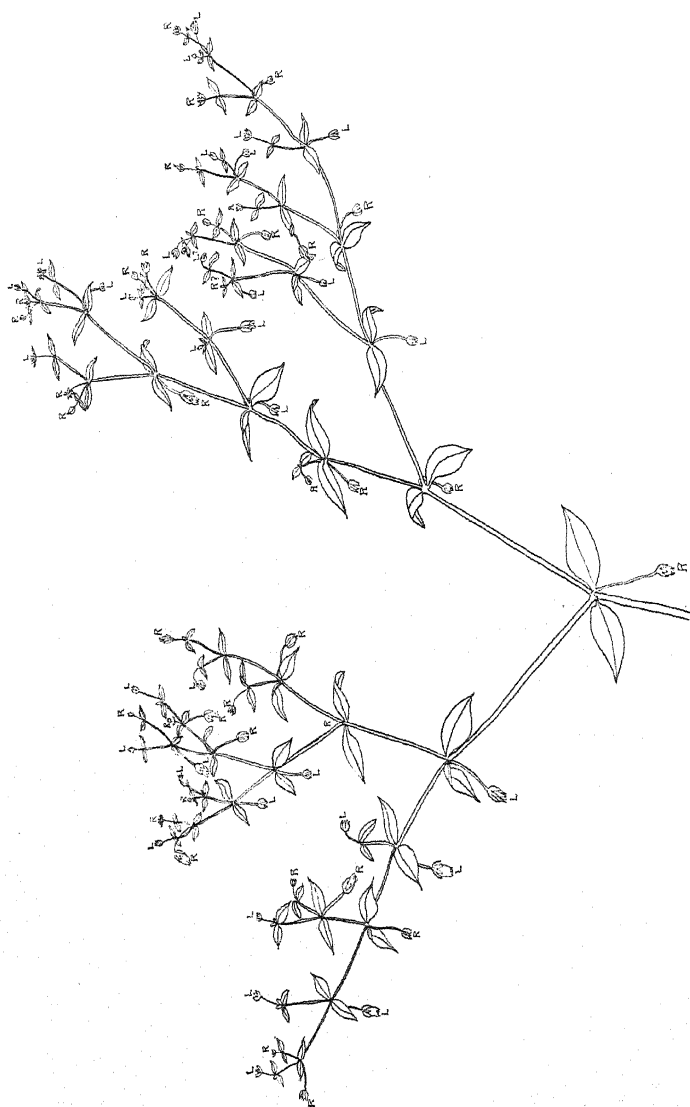


Fig. 5a. An actual inflorescence of *S. aquatica* ($\times 1/3$). Explanation in the text.

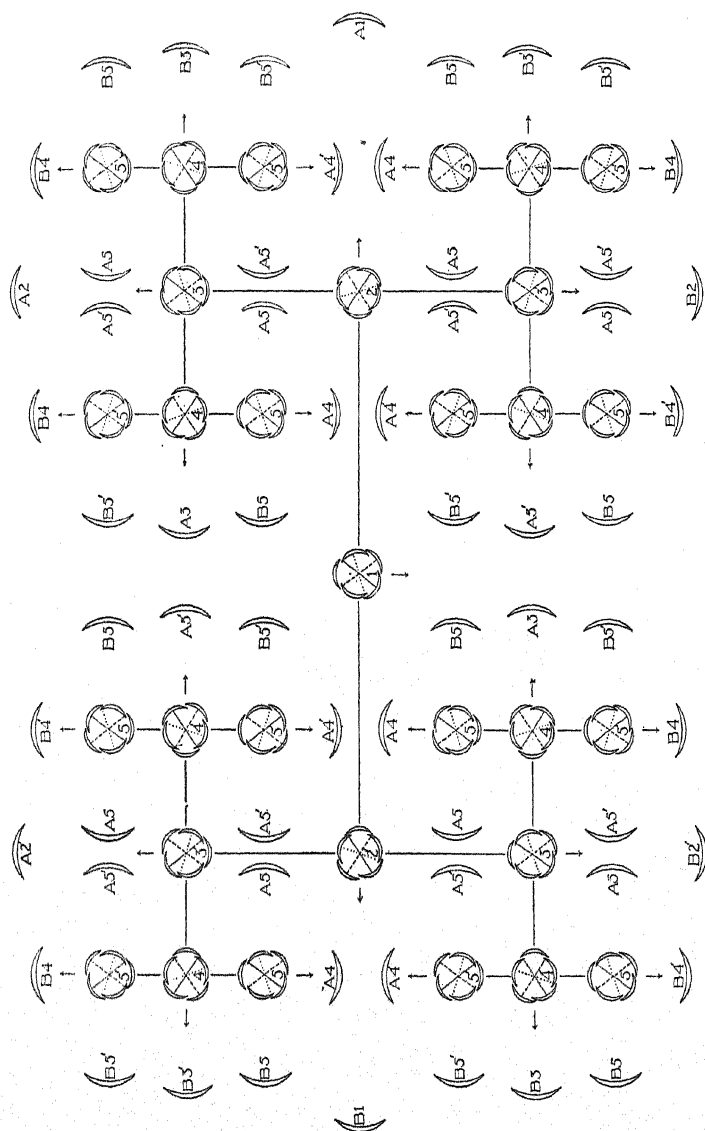


Fig. 5b. Diagram of an inflorescence of *S. aquatica*. Explanation in the text.

sequence as in figure 7. The flower terminating the branch in the axil of bract *A* in figure 7 will have the sepals originating in counterclockwise sequence; and that terminating the branch of bract *B* in figure 7 will have the sepals originating in clockwise sequence. Thus these branches are just opposite in this respect in figures 6 and 7. Each of these branches in turn produces two branches at its only node; these also have but a single additional node and a flower, that terminating the one branch having the sepals as in figure 6, that terminating the other having the sepals as in figure 7. This is shown more clearly in the diagram of the cyme in figure 5b, where these relationships can readily be followed. There the flowers are numbered, and the bracts associated with a flower have the same number as that flower. Thus bracts *A*1 and *B*1 are at the base of the pedicel of flower number 1. Flowers having the sepals originating in clockwise sequence are indicated with a ' ; and flowers terminating branches arising at the same or similar nodes in the inflorescence have the same number.

A rule for determining these relationships which can be followed is to stand with the reflexed pedicel of the flower (reflexed after anthesis) toward you. The flower of the branch on your right (marked *R* in figure 5a) of the node above the reflexed pedicel will then usually have the sepals overlapping as in figure 7; the flower of the branch on your left (marked *L* in figure 5a) of the node above the reflexed pedicel will then have the sepals overlapping as in figure 6. Furthermore the bract toward you of the node above the reflexed pedicel on the branch on your right will be bract *B* in figure 7; the bract toward you of the node above the reflexed pedicel on the branch on your left will be bract *B* in figure 6. Bracts *A* in both cases will be on the sides of the branches away from you. The pedicels of each of these flowers will become reflexed after anthesis and a branch will originate in the axil of each of their subtending bracts; the same rule can then be applied there. All this is also evident from figure 5b. In that figure the direction of the bending of the pedicels is indicated by arrows.

Exceptions to the general rules laid down above are rather frequent. Of 373 flowers (excluding the first of a cyme) examined while they were open, 24 did not conform. A common condition was to have both of the branches originating

at the same node in an inflorescence terminated by flowers with the same sepaline arrangement, instead of having the sepals of one flower as in figure 6, of the other as in figure 7. In some instances both branches had flowers with the sepals as in figure 6, in others both flowers had the sepals as in figure 7.

The pedicels after anthesis will bend in a definite fashion. If the flower they support has the sepals as in figure 6 they will bend so that they are more or less parallel with the midvein

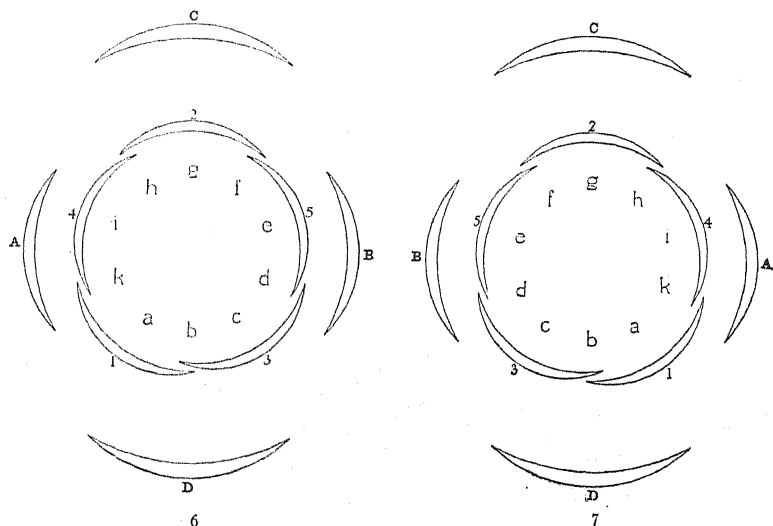


Fig. 6. Arrangement of the bracts and of the sepals in a flower in which the latter originate in clockwise sequence. Fig. 7. Arrangement of the bracts and of the sepals in a flower in which the latter originate in counter-clockwise sequence.

of bract *D* of the node below; this is equivalent to saying that if a pedicel supports a flower having the sepals as in figure 6, it will bend so that it is more or less parallel with the midvein of bract *A* of the node below, provided this latter bract subtends a flower with the sepals as in figure 6, since bract *A* in that case becomes bract *D* with reference to that node above. If this flower of the node below has the sepals as in figure 7, then the pedicel supporting a flower having the sepals as in figure 6 will bend after anthesis so that it is more or less parallel with the midvein of bract *B* of that node below.

If, on the other hand, a pedicel supports a flower having the sepals as in figure 7, it will bend after anthesis so that it is more or less parallel with the midvein of bract *D* of the node below; in other words, if a pedicel supports a flower having the sepals as in figure 7, it will bend so as to become more or less parallel with the midvein of bract *A* of the node below, provided this latter bract subtends a flower with the sepals as in figure 7. If this flower of the node below has the sepals as in figure 6, then the pedicel supporting a flower having the sepals as in figure 7 will bend after anthesis so that it is more or less parallel with the midvein of bract *B* of the node below.

This spatial configuration persists throughout the inflorescence; it is shown diagrammatically in figure 5b; it is shown also in figure 5a, which is a drawing of an actual specimen, slightly schematized in that the slight twistings of the internodes have been somewhat disregarded to give greater clarity.

In the inflorescence, as in the vegetative branching, there may be poorly developed branches, or branches may fail to develop entirely. If one of the two branches originating at a flowering node is less developed than the other, it will as a rule be the one terminated by the flower whose calyx is homodromic with that of the flower subtended by the bracts in the axils of which both branches originate. Thus in figure 6 the flower will bend toward bract *D* after anthesis; the branch in the axil of bract *A* will be terminated by a flower whose sepals are homodromic with those of figure 6; that in the axil of bract *B* will be terminated by a flower whose sepals are antidromic with those of figure 6. If one of these two branches is poorly developed it will as a rule be that in the axil of bract *A*. If one of these two branches fails to develop entirely it will also be the one in the axil of bract *A*. If one of the bracts subtending the flower in figure 7 had a weakened branch in its axil it would be bract *A*; and if only one branch develops it will be the one in the axil of bract *B*. This applies to any part of the inflorescence, as may be deduced from figure 5a. There it is evident that if a branch of the inflorescence is poorly developed or fails to develop entirely it will as a rule be the one terminated by a flower whose calyx is homodromic with that of the flower in the axil of whose bract this branch originated. In figure 5a the relative length of the internodes is just as it was in the

actual specimen. Of 51 recorded observations on the failure of one of the branches at a node to develop, only one was not according to the rule formulated above. It is not unusual to find two branches at a node and no flower, a flower and no branches, a flower and one branch, or a flower and one small and one large branch.

THE FLOWER

In comparison with the flowers of *Stellaria media* those of *S. aquatica* are relatively stable with reference to the number of parts. But even in *S. aquatica* there is considerable variation; and since the variability seems to be due in part at least to reduction of parts, a study of a form in which reduction is manifested to only a limited extent might show the early stages of reduction. The data given below have been accumulated with the intention of determining whether the variations occurring in this species are as unordered as might at first appear, and of determining as far as possible the range and limitations of these variations.

No microscopical examination of the stages in the development of the flower has been made in this study to determine the exact relationship between the bracts subtending the flower in the bud, and the sepals. This relation was studied in 65 cases in which the flower had opened; this is not very satisfactory, since there is often a twisting of the pedicel of the flower which obscures the true relationship. The results obtained are in essential agreement with those of Wichura (1846, 1847). Wichura's figures are similar to those of later authors (Eichler, 1878; Warming, 1904; Béguinot, 1920). Eichler's figure has been widely adopted, among others by Pax (1889) and Rendle (1925).

As mentioned above, the overlapping of the sepals may be of two types, depending upon their origin, in clockwise sequence as in figure 6, and in counterclockwise sequence as in figure 7. Branches having the smaller branches upon them in clockwise spiral are terminated by flowers whose sepals originate in counterclockwise sequence; those having the smaller branches in counterclockwise spiral are terminated by flowers whose sepals originate in clockwise sequence. Of 1180 flowers examined, 579 had the sepals originating in clockwise sequence

(as in figure 6), 601 in counterclockwise sequence (as in figure 7). This difference is not very striking, but, as shown above, there were also more branches having the clockwise arrangement of their smaller branches and hence the counterclockwise sequence of the sepals in their first flowers.

The typical flower of *S. aquatica* is pentacyclic, pentamerous, and syncarpous. As indicated in table 3, however, there is considerable variation from this type. The data shown there were obtained from plants growing wild. In the vicinity of the city of New York the flowering period begins about the first week in July and extends to the end of November or beginning of December.

a. *The calyx.* The sepals varied in number from four to six—a rather small range. There is no time during the flowering period in which the number varies greatly. In table 3 there is shown a slight increase in the number of sepals in the beginning of October, but whether this is of any significance is questionable. Of all the parts of the flower the sepals showed the least variation in number—27 flowers with four sepals, 3756 with five, and 7 with six, making a total of 34 with other than five sepals against 3756 with five, or less than one per cent.

The size of the sepals varies greatly, the first formed in an inflorescence usually being about 8 mm. long in fruit. Those later formed are smaller; in flowers with sterile stamens they are often much smaller, and in completely sterile flowers they are sometimes hardly more than a millimeter in length or even less.

Four-sepaled flowers are in general of two kinds: those in which all or nearly all the parts are in multiples of four, and those in which the remaining parts are in multiples of five. In the latter there is obviously a fusion of two sepals, or the formation of one sepal of approximately twice the dimensions of a typical sepal. A study of the vascular system has been made (to be published shortly), which shows that the internal structure is correlated with the two kinds of four-sepaled flowers indicated above, and that the difference is not merely superficial. Figure 16 is a diagram of a flower with four sepals all of the characteristic form; in figure 17, on the other hand, all parts of the flower are regular except one sepal which is obviously double the normal size, and has three stamens and

a petal opposite it instead of a single stamen. These diagrams, as well as all the others, are representations of actual flowers, and the two just discussed are not uncommon. Figure 18 shows a case in which all four sepals are apparently normal, none is appreciably larger than the others; whether one of the sepals was supplied with double the amount of vascular tissue, whether one of them has become entirely petaloid, or whether the internal parts correspond with the external appearances remains to be investigated. It is not unusual in four-sepaled flowers to have only nine stamens, and sometimes three-lobed petals occur.

Two additional factors support the view that the large sepals described above are in reality two sepals fused; first the occurrence, rather rarely, of a single large sepal more or less two-lobed, indicating partial fusion; and secondly the fact that different sepals are apparently fused at different times. The commonest arrangement in flowers having four sepals, one larger than the others, is to have two inner sepals alternating with two outer, sepal 3 of figures 6 and 7 being apparently eliminated. One of the inner sepals then is twice its normal size, suggesting that there has been a fusion of sepals 3 and 5 of both figures. This is illustrated in figure 17. In two flowers the calyx consisted of an outer sepal, then (going in clockwise direction) an oblique one, like sepal 3, this being double, then an inner sepal, then another oblique one, suggesting that sepals 4 and 2 in figure 6 had fused. In another flower the arrangement, in clockwise fashion, was an oblique sepal (double), an outer sepal, another oblique sepal, and an inner sepal, indicating that sepals 2 and 4 of figure 7 had fused; all the other parts of the flower were in multiples of five. This evidence indicates strongly that there can be fusion of different sepals, the oblique one (number 3) with an inner, or an outer with an inner sepal.

Sometimes in the calyx of *S. aquatica* there are sepals that are partially petaloid. This may be evident as merely a fine white line appearing in the center or on one side of the sepal; in other cases there are two white lines; from this there are all gradations to that condition in which the sepal is a two-lobed structure, one lobe of which is white, to that in which practically the whole sepal is white and two-lobed with just a trace of

green. The sepal affected in 40 flowers in which one was more or less petaloid in character, was in each case one of the inner ones; and of the 40 instances, sepal number 4 was affected 12 times, sepal number 5, 28 times; this shows that the sepal nearest the petaline whorl in origin most frequently becomes more or less petaloid. One flower (fig. 18) was observed having four sepals all apparently normal, but between two there were three petals; it is possible that the middle petal of these three was a transformed sepal; the positions of the styles would substantiate this though there were only nine stamens. This is merely a suggestion and awaits further histologic investigation. This discussion of the petaloidy of the sepals is not offered as anything new; nevertheless it is intimately associated with the question of the origin of the perianth, a problem that has been debated up to the present but not wholly settled.

b. *The corolla*. Greater variation in both range and numbers was shown by the petals than by the sepals. There were 20 flowers with four petals, 3721 with five, 46 with six and 3 with seven. Here again there seems to be no time during the flowering period at which the number of petals is decidedly greater or less than at any other, though there was considerably more variation in August than at any other time; but the number of individuals was not very large for such a study.

By means of sepal 3 it is possible to determine the position in the flower in which additional petals most frequently occur. The number of times that additional petals occurred in each position in figures 6 and 7 is shown in tables 4 and 5. It is evident that additional petals very rarely occur opposite the sepals. Supernumerary petals usually occur between sepals 2 and 4, at position *h* in both figures. The additional petals at *h* numbered 32, those at all the other positions combined totaled only 18. The occurrence of additional petals in position *h* is shown in figures 19, 20, 21, and 23. It is thus possible to predict where in the flower extra petals will usually occur.

Of 46 flowers with one additional petal, 27 also had an additional stamen opposite that petal, fourteen had just one stamen associated with the two petals, four had no stamens with either petal, and one had three stamens with the two petals. In the greater number of cases, then, there is an additional stamen opposite an additional petal. This rather emphasizes

the close relationship between stamens and petals. Limited data indicate that when a petal is missing the stamen usually develops just the same. But this point needs further investigation.

Three flowers having seven petals showed considerable variation in the distribution of the latter; one flower had two additional petals between the same two sepals, another had two on each side of a single sepal (instead of just one), and the third had six sepals with two petals between one pair.

TABLE 4

Number of additional petals and additional, missing, and sterile stamens in each position in flowers having the sepals arranged in counterclockwise sequence as in figure 7

SEPAL NO.	1		3		5		2		4		TOTAL NUMBER	
POSITION IN FLOWER	a	b	c	d	e	f	g	h	i	k	Alternate with sepals	Opposite sepals
Additional petals		4		4			2	22	1	1	31	3
Additional stamens	1	4		2	3		1	19	10	1	26	15
Missing stamens	1	2		2	2	13	1	3		1	21	4
Sterile stamens	103 (108.5)	109 (114.8)	64 (67.4)	63 (66.4)	52 (54.8)	101 (106.4)	92 (96.9)	119 (125.4)	90 (94.9)	141 (148.5)	533	401

Petals having three lobes instead of two not infrequently occur. Sometimes one of the three lobes is smaller than the others (usually the central one); in other cases the three are all of approximately equal size. Of five five-sepaled flowers like that in figure 7, having a three-lobed petal, four had it in position *h*. Of four flowers like that in figure 6, three had the three-lobed petal at *h*, making a total of seven out of nine possible cases at *h*; the other two positions were *d* in figure 7 and *b* in figure 6. The position *h* is the one in which additional petals also most frequently occur. There were also two four-sepaled flowers having three-lobed petals. Of eleven flowers having three-lobed petals, six had a single stamen associated with the three-lobed petal, five had two stamens, showing that it is not unusual to have an increase in the number of stamens associated with an increase in the petal quantity.

Simple petals (not two-lobed) are also found in *S. aquatica*.

There were nine such cases observed, one occurring at points *h* and *b* in figure 7, one at *h* and *k* and five at *d* in figure 6. Such petals were associated with a single stamen, as in the case of normal petals.

In addition to these non-lobed petals, others sometimes occur in which the lobes are of unequal size. Then too there are flowers in which the petals are much reduced in size. This is particularly true of the flowers with sterile stamens produced especially toward the end of the year; in these the corolla may be no larger than the calyx, and sometimes it is decidedly smaller.

TABLE 5
Number of additional petals and additional, missing, and sterile
stamens in each position in flowers having the sepals
arranged in clockwise sequence as in figure 6

SEPAL NO.	1		4		2		5		3		TOTAL NUMBER		TOTAL tables 4 and 5	
POSITION IN FLOWER	a	k	i	h	g	f	e	d	c	b	Alternate with sepals	Opposite sepals	Alternate with sepals	Opposite sepals
Additional petals		3		10				3			16	0	47	3
Additional stamens			6	9			1	1	1		10	8	36	23
Missing stamens		2		2	2	5	1			2	11	3	32	7
Sterile stamens	115	135	99	118	109	112	65	68	69	94	527	457	1060	858

Sometimes one or several of the petals are reduced, while the others are of the normal size. There may thus be petals of different sizes in the same flower. The most extreme reduction takes place in the minute totally sterile flowers in which the petals are sometimes reduced practically to the vanishing point.

Petals more or less green (usually less) have been observed. This is a suggestion of sepaline character. Further suggestion of the relationship between sepals and petals is offered by the occurrence of two-lobed sepals with one lobe green and the other white, with the petal missing which should be adjacent to the white half of the sepal. Whether such instances are cases of fusion between members of the two whorls remains to be established for *S. aquatica*.

Anthers sometimes occur on petaloid structures. This was observed in only four cases in this species, and in each of these the petaloid structure was in addition to the usual number of petals. In one instance the stamen, anther and filament, were apparently fused with a petaloid structure, as all were distinguishable. In the other three the anthers were simply borne on a petaloid outgrowth, simple in two cases, two-lobed like a petal in the other. In each instance there was the usual complement of ten stamens also, so that these structures were supernumerary with regard to both petals and stamens. Whatever interpretation may be placed upon them, their occurrence further emphasizes the close relationship between stamens and petals.

c. *The androecium*. The number of stamens varies decidedly more than that of the sepals and petals, as indicated in table 3. Of 3790 flowers 7 had eight stamens, 62 had nine, 3667 had ten, 51 had eleven and 3 had twelve. The ten usual stamens are arranged five opposite the sepals and five opposite the petals. In the floral diagrams below they have been drawn as two whorls in the obdiplostemonous arrangement. The question of obdiplostemony is to be considered further in the study of the internal structure of the flower. Each of the antesealous stamens is provided with a gland at the base of the filament.

As indicated in tables 4 and 5 the positions in each of the two kinds of flowers in which additional stamens most usually occur are *h* and *i*. Of 41 supernumerary stamens occurring in flowers having the sepals in counterclockwise sequence 19 were at *h* and 10 at *i*; and of 18 additional stamens in flowers in which the sepals originated in clockwise sequence 9 were at *h* and 6 at *i*. Out of a possible 59, 44 of the additional stamens occurred in these two positions; additional stamens at *h* were more frequent than at *i*. The close proximity of these two positions may also be of significance. Figures 19, 20, 24, 25, and 26 illustrate the occurrence of extra stamens in these positions.

Position *h* is important, then, because it is there that additional petals, three-lobed petals, and additional stamens most frequently occur. Furthermore position *h* with the center of sepal 3 establishes an axis passing through the center

of the flower. This axis corresponds in position with axes of symmetry in the flowers of *Hyoscyamus albus*, *Stigmaphyllon*, *Hiptage Madablota*, *Camarea triphylla*, *Trigonía simplex*, *Hirtella triandra*, *Couepia macrophylla*, *Licania macrophylla*, *Parinarium Gardneri*, and *Hirtella Sprucei* (Eichler 1875, 1878).

Of 36 supernumerary stamens opposite petals, 27 were associated with an additional petal, 4 with a three-lobed petal (the fifth three-lobed petal mentioned above being in a flower having nine stamens) and in only 5 cases were two stamens associated with a single petal. This again emphasizes the close relationship between these structures. It is not unusual to find two stamens opposite a sepal and then there is no additional petal or sepal.

The position at which a stamen may most easily be lost also seems to be relatively fixed. As indicated in tables 4 and 5 position *f* more frequently is without a stamen than any other. In 18 cases out of 39 this was the position affected. In only 7 instances out of 39 was a sepaline stamen lost. The failure of a stamen to develop in position *f* is shown in figures 27 and 28. With the center of the flower position *f* establishes another axis; this is similar in position with axes of symmetry in the flowers of *Petunia nyctaginiflora*, *Schizanthus retusus*, *Salpiglossis sinuata*, *Anacardium occidentale*, *Saxifraga granulata*, *Saxifraga sarmentosa*, and *Cassia caroliniana* (Eichler 1875, 1878). Through these axes, shown in figure 5b, which are established in the flower with a certain amount of constancy, the flower seems to be losing its regularity and taking on a form which, to a certain extent at least, is zygomorphic with respect to certain whorls.

Eight stamens have been found in four- and five-sepaled flowers, nine in four-, five-, and six-sepaled flowers, ten in four- and five-sepaled flowers, eleven and twelve in five- and six-sepaled flowers.

When a stamen is missing it frequently happens that the filament of one of the adjacent stamens, instead of being more or less in a plane with the axis of the flower, leans over into the space in which the stamen is missing, the anther sometimes being extended beyond the place that the missing stamen would occupy.

Sterility in the androecium. Flowers of *S. aquatica* frequently

have one or more of the stamens modified into staminodia. There are all grades in the sterility of the stamens. All the normal anthers examined showed some small pollen grains. From this condition of normal minimum which seems to prevail in all flowers there are examples of all grades in the increase in the proportion of sterile grains to cases in which the majority of the grains in an apparently normal anther are small and shrivelled. Likewise there are stamens which have normal anthers with the usual proportion of normal grains but with the filament shortened; or the filament may be of the usual length but the whole anther shrivelled and dry in appearance. Such anthers have a fraction at least and more usually all of the grains shrivelled. There are examples of all stages in the decrease in the size of the anthers, from those only slightly below normal to those in which the anther consists merely of an extremely minute membranous structure without pollen grains; sometimes there appears to be a yellow mass within the anther, not developed into grains; sometimes this too is lacking. This reduction of the anthers is accompanied as a rule by a reduction in the size of the filaments, so that sterile stamens are often very small structures barely visible to the naked eye; sometimes they appear merely as minute microscopic papillae. It occasionally happens that half an anther is normal with normal grains, the other half small with shrivelled grains.

Preliminary germination tests which have been made indicate that the small shrivelled grains do not germinate under conditions identical with those permitting the formation of tubes in the normal grains.

Tables 4 and 5 show the positions of the staminodia in flowers having from one to nine stamens sterile; all are here grouped together except those having all ten stamens sterile. Table 4 was compiled from 305 flowers having a total of 934 staminodia, or 3.06 staminodia per flower; table 5 gives data from 300 flowers having a total of 984 staminodia or 3.28 staminodia per flower, giving an average of 3.17 staminodia per flower.

In the flowers examined the production of reduced stamens was more common in the antepetaline than in the antesepaline whorl—a total of 1060 sterile stamens in the former to 858

TABLE 6
Sterile stamens in Stellaria aquatica

DATE	NUMBER OF FLOWERS WITH THE FOLLOWING NUMBER OF STERILE STAMENS										Number of flowers with sterile stamens	Number of sterile stamens on re- spective days	Number of flowers examined on re- spective days	Per cent of flowers examined with sterile stamens	Total number of stamens on re- spective days	Per cent of stamens sterile
	1	2	3	4	5	6	7	8	9	10						
July 8	—	—	—	—	—	—	—	—	—	—	0	0	18	0	180	0.0
" 14	1	—	—	—	—	—	—	—	—	—	1	1	90	1	902	0.1
" 18	—	—	—	—	—	—	—	—	—	—	0	0	100	0	998	0.0
" 20	6	—	—	—	—	—	—	—	—	—	6	6	100	6	1001	0.6
" 22	—	1	1	3	—	2	—	—	—	—	10	50	100	10	998	5.0
" 26	—	—	1	2	1	—	—	—	—	—	4	16	100	4	1002	1.6
" 28	3	3	3	—	—	2	—	—	—	—	11	30	100	11	997	3.0
Aug. 4	4	—	—	1	1	—	2	—	—	—	8	27	100	8	1000	2.7
" 8	2	—	—	1	1	2	—	1	—	—	8	41	100	8	1006	4.1
" 17	7	4	1	3	1	1	—	1	—	4	22	89	100	22	1003	8.9
" 20	—	1	1	1	—	—	—	—	—	—	5	25	100	5	1005	2.5
" 22	8	6	3	4	3	3	1	—	1	3	32	124	101	32	1007	12.3
" 25	5	1	1	—	2	—	—	—	—	—	9	20	100	9	1003	2.0
" 31	—	1	1	—	—	—	—	—	—	—	2	5	70	3	703	0.7
Sept. 8	1	5	4	1	1	2	1	3	1	1	20	94	37	54	369	25.5
" 9	3	2	—	—	1	1	—	—	—	3	10	48	15	67	150	32.0
" 27	4	6	1	2	—	1	—	—	2	1	17	61	91	19	911	6.7
" 28	3	4	1	3	2	—	2	—	3	2	20	97	88	23	878	11.0
" 29	8	3	2	2	1	—	1	1	—	—	18	48	100	18	1000	4.8
" 30	5	—	3	3	—	—	—	—	—	—	11	26	105	10	1045	2.5
Oct. 1	5	—	6	4	3	1	2	—	—	—	21	74	83	25	826	9.0
" 2	2	4	4	—	—	—	—	3	—	—	14	52	66	21	656	7.9
" 3	7	—	3	2	3	1	—	—	—	1	17	55	85	20	845	6.5
" 4	11	3	2	1	—	1	3	—	—	—	21	54	113	19	1125	4.8
" 5	7	5	2	4	1	—	—	1	—	1	21	62	104	20	1039	6.0
" 6	6	4	1	1	1	1	—	—	—	—	14	32	112	13	1120	2.9
" 7	7	1	2	—	1	—	1	—	—	—	12	27	50	24	500	5.4
" 8	2	1	—	—	—	—	1	1	—	—	6	29	37	16	368	7.9
" 9	9	2	4	3	1	2	1	6	1	3	32	148	109	29	1087	13.6
" 12	6	7	3	—	1	1	1	2	—	2	23	83	119	19	1190	7.0
" 13	12	3	2	3	—	—	1	—	—	1	22	53	133	17	1330	4.0
" 14	2	1	1	1	2	1	—	—	—	—	8	27	107	7	1071	2.5
" 16	3	—	—	2	1	—	2	1	—	—	9	38	98	9	979	3.9
" 18	5	6	3	2	2	—	1	—	—	—	19	51	44	43	440	11.6
" 20	7	3	1	1	—	—	—	—	—	—	12	20	91	13	911	2.2
" 23	5	4	1	1	1	1	—	—	—	—	13	31	100	13	1000	3.1
" 27	4	—	1	1	—	—	1	1	—	—	8	26	53	15	530	4.9
" 28	7	3	1	1	1	—	—	—	—	1	14	35	94	15	940	3.7
" 31	3	1	5	1	3	1	—	—	2	3	19	93	43	44	429	21.7
Nov. 2	1	5	4	3	3	3	1	1	—	—	21	83	64	33	640	13.0
" 4	4	6	1	2	1	—	2	2	—	6	24	122	77	31	770	15.8
" 7	2	7	2	2	—	1	2	—	—	2	18	70	62	29	622	11.3
" 10	4	2	1	1	4	1	1	1	1	10	26	165	49	53	491	33.6
" 11	2	6	3	2	3	3	1	1	—	3	24	109	46	52	460	23.7
" 14	7	6	2	3	2	1	2	1	—	—	24	75	42	57	421	17.8
" 17	6	—	—	1	—	—	—	—	—	—	7	10	10	70	100	10.0
" 18	3	3	—	3	1	—	—	1	—	—	11	34	20	55	200	17.0
" 19	3	1	2	—	1	—	—	—	—	2	10	42	15	67	150	28.0
" 21	2	1	1	2	—	1	—	—	1	2	10	50	15	67	150	33.3
" 22	—	—	—	1	—	—	—	1	1	1	4	31	10	40	99	31.3
" 25	1	1	1	—	—	—	1	2	1	—	7	38	7	100	70	54.3
" 27	2	—	—	1	—	—	1	—	—	—	4	13	6	67	58	22.4
" 28	1	1	—	1	—	—	—	—	—	1	4	17	5	80	49	34.7
Dec. 1	1	—	—	—	—	—	1	—	—	2	4	28	6	67	60	46.7
Totals	210	124	82	76	50	37	33	31	14	60	717	2685	3790	19	37884	7.1

in the latter. Tables 4 and 5 show further the number of these in each position in the flower, the letters being the same as in figures 7 and 6. In ascending order with reference to the number of sterile stamens the positions in table 4 are *e, d, c, i, g, f, a, b, h, k*; the order in table 5 is *e, d, c, b, i, g, f, a, h, k*. These orders, excepting *b* are the same. The total number of sterile stamens taken into account in tables 4 and 5 is 1918, of which 934 are in table 4 and 984 in table 5. Therefore each of the

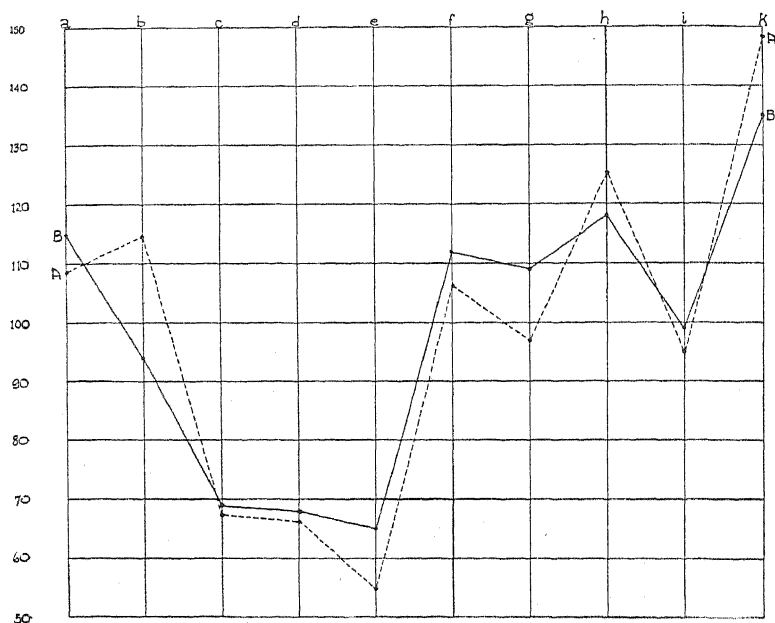


Fig. 8. Frequency of the occurrence of sterile stamens, *AA* of the positions of the flower having the sepals as in figure 7, *BB* of the positions of the flower having the sepals as in figure 6.

figures in table 4 was multiplied by $984/934$, and the values obtained are recorded in parentheses. Then these values and those of table 5 were plotted as shown in figure 8. There *AA* is the graph for table 4, *BB* the graph for table 5. The general similarity of these curves is quite evident, the greatest inconsistency being at *b*. Why certain positions should have more or fewer sterile stamens, in definite ratio with the other positions, is not evident.

Table 6 gives the number of flowers with 1-10 sterile stamens for different days during the flowering period. Thus on July 22, there was one flower with one sterile stamen, one with two, one with three, three with four, none with five, two with six, none with seven, eight and nine, and two with all ten stamens sterile, giving a total of ten flowers showing one or more sterile stamens and a total of 50 sterile stamens for those ten flowers. The total number of flowers examined on that day was 100 and the total number of stamens on those 100 flowers was 998. Therefore the percentage of flowers showing one or more sterile stamens was

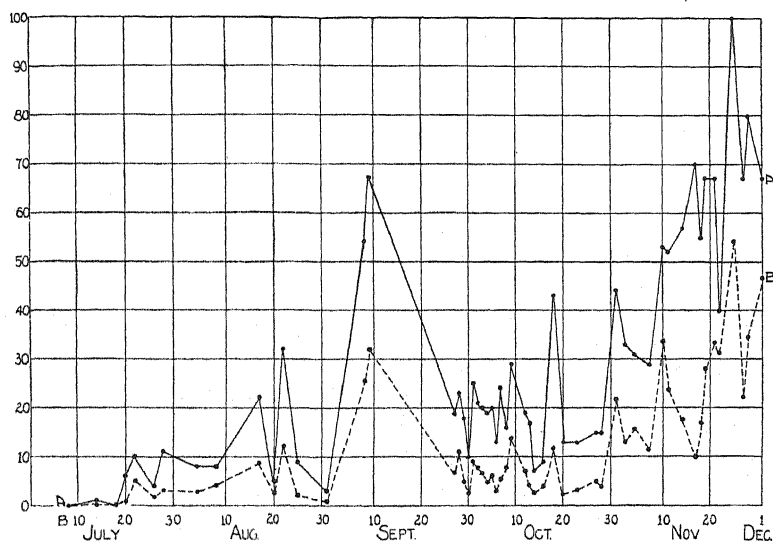


Fig. 9. Advancing seasonal staminal sterility: *AA* the per cent of the total number of flowers examined on the respective days with one or more sterile stamens, *BB* the per cent of the total number of stamens on the respective days sterile.

10; the percentage of the total number of stamens sterile on that day was 5.0. These percentages are shown plotted in figure 9, *AA* being the percent of the total number of flowers examined on the respective days with one or more stamens sterile, *BB* the per cent of the total number of stamens sterile each day. The average of the first taking the total number of flowers into account, was 19 per cent, that of the second 7.1 per cent.

In general there is a gradual increase in the number and

proportion of sterile stamens toward the end of the season. The only striking exception to this general increase was on September 8 and 9. It should be stated that torrential rains during the first week in September washed away all but the older and lower portions of a few plants; this also explains the small number of flowers examined on those days. Some of the other smaller deviations are less easily explained. The plants were growing wild and not all in the same place; the flowers were taken at random. Those for instance listed for October 18 were found in a more exposed place, and were apparently more liable to insect attack than the others. Some variations are to be expected, but the general trend, with the one exception mentioned above, can hardly be questioned. There is apparently a gradient here associated with metabolic activity (Child, 1915a, b). The terms sterile and reduced are used in their broadest sense, any stamen showing some evidences of sterility being listed.

It is apparent from table 6 that the number of flowers having just a single stamen sterile is greater than that of flowers having two, and that the number of flowers decreases as the number of staminodia increases, excepting in flowers having all ten stamens sterile; there, there was a decided increase. Such flowers having all the stamens sterile are really imperfect. A limited number of these was cross pollinated and set seed in each case, while similar flowers not pollinated did not. Both Henslow (1888) and Rendle (1925) ascribe the derangement of the staminal whorls to low temperature, Rendle remarking that in *S. media* 'the number of abortive stamens is greater the colder the time of year.' This is in agreement with the results given above. However they go on to say that in the Alsinoideae the pistillate flowers are in bloom chiefly at the beginning of the flowering period. This does not hold for *S. aquatica*. Plants growing wild in the vicinity of the city of New York have been watched for several years. They did not come into bloom much if any before the first week in July. Of a total of 608 flowers gathered at random during the month of July only two had all ten stamens sterile, while in November of 428 flowers 27 had all the stamens sterile. This indicates that for *S. aquatica* the condition is just the reverse of that given by Henslow and Rendle for the Alsinoideae.

d. *The gynoeceium*. The styles and carpels of *S. aquatica* are typically five in number. Bentham (1861, 1862) however, reported the occurrence of three-styled flowers in India and temperate Asia. Béguinot (1914) gives the variations in the number of styles from six to two, four and three being the most common after five. He remarks that the percentage of flowers with four styles is greater in June and July and less in October and November.

The number of styles in flowers recorded in table 3 varied from three to seven, there being 13 flowers with three, 256 with four, 3409 with five, 107 with six and 5 with seven. The proportion of four-styled flowers here is less than that reported

TABLE 7
Variation in number of styles according to months

MONTH	NUMBER OF FLOWERS EXAMINED	NUMBER OF 4-STYLED FLOWERS	PER CENT OF FLOWERS 4-STYLED	NUMBER OF 6-STYLED FLOWERS	PER CENT OF FLOWERS 6-STYLED
July	608	14	2.3	21	3.4
August	671	52	7.7	16	2.4
September	436	55	12.6	9	2.1
October	1641	107	6.5	41	2.5
November	428	28	6.5	19	4.4
Totals	3784	256	6.8	106	2.8

by Béguinot, and the proportion of six-styled flowers much greater. The four-styled flowers examined by Béguinot varied in number from approximately 28 per cent of the total number in June and July to 13.24 per cent in October and November, and only 3 out of 814 flowers were six-styled. In table 7 the data given in table 3 are arranged according to months; in contrast to the figures for the Mediterranean region the data for New York indicate a variation in the proportion of four-styled flowers from 2.3 per cent in July to 12.6 per cent in September, the proportion of the total number of flowers four-styled being 6.8 per cent. Of course the variation in the months, if seasonal, would not correspond with that in Italy and the Mediterranean countries. The percentage of six-styled flowers varied from 2.1 to 4.4 per cent, the proportion of the total

number of flowers six-styled being 2.8 per cent. Thus the percentage of six-styled flowers, while low, was not entirely negligible, and in July actually exceeded that of the four-styled flowers. The proportion of three-styled flowers found is less than that reported by Béguinot.

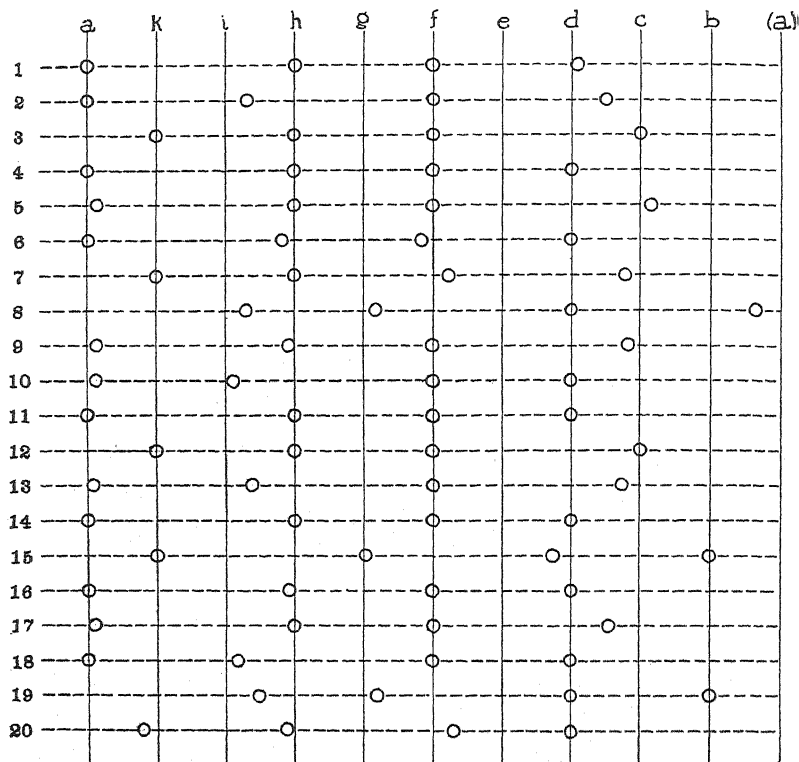


Fig. 10. Position of the styles in 20 four-styled flowers having the sepals overlapping as in figure 6.

The five styles of *S. aquatica* typically alternate with the five sepals i.e. the carpels are opposite the petals. Therefore in four- and six-styled flowers there must of necessity be some asymmetry. In figures 10 and 11 the positions of figures 6 and 7 are plotted and lettered as in those figures. The circles in those figures represent the styles, each of the flowers there diagrammed having four. Figure 10 thus shows the positions of the styles in 20 four-styled flowers; in figure 11, 21 flowers are represented.

In the normal five-styled flower there is a style in positions *b*, *d*, *f*, *h*, *k*. The data here presented are subject to some error because of the bending of the styles and stigmas. However by examining the styles near the base this difficulty is partly overcome at least. This procedure was followed. The splitting of the capsules was in many cases compared with the positions

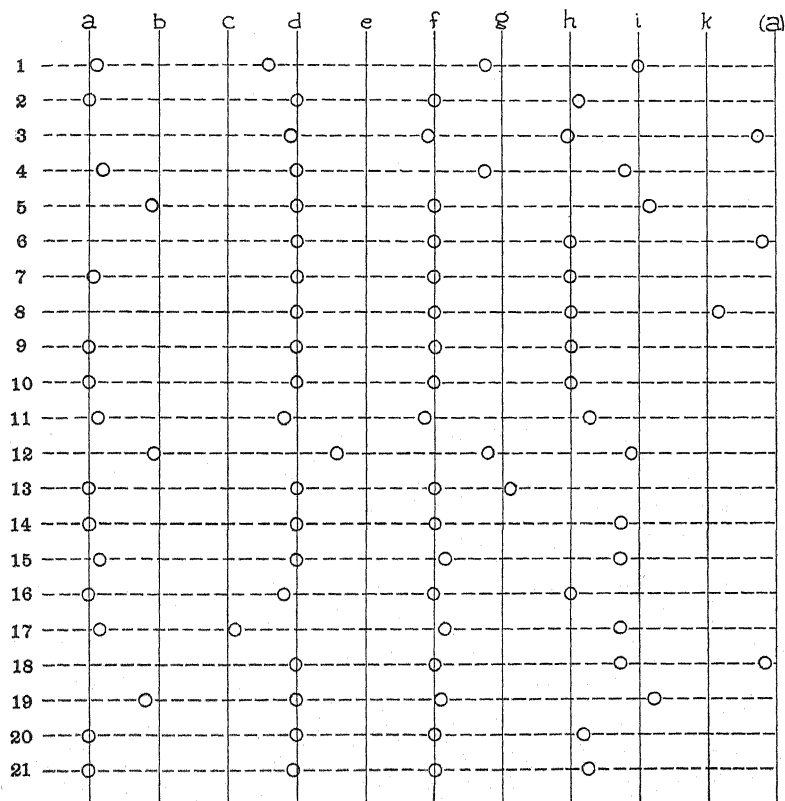


Fig. 11. Position of the styles in 21 four-styled flowers having the sepals overlapping as in figure 7.

of the styles (by means of records) and there was general agreement in the major lines of splitting, with some exceptions. From figures 10 and 11 it is evident that in a general way the styles primarily affected in four-styled flowers are those in positions *b* and *k*; these are usually replaced by a single one

which varies somewhat in its position but tends to be at or near position *a* (shown also in figure 29). This holds for flowers with the sepals overlapping as in figures 6 and 7 in equal measure. Position *a* with the center of the flower also establishes an axis in the flower; this axis is identical in position with the one established by the frequent loss of a stamen in position *f*.

Figures 12 and 13 show the positions of the styles in six- and seven-styled flowers. From figure 13 it appears that the single style at *d* tends to be replaced by one at both *c* and *e*,

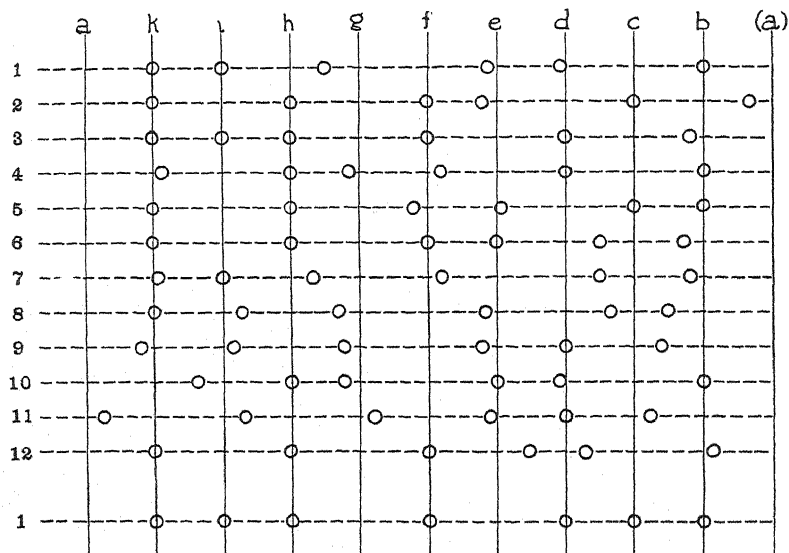


Fig. 12. Position of the styles in 12 six-styled flowers and 1 seven-styled flower having the sepals overlapping as in figure 6.

thus accounting for the additional one (fig. 30). Of course the position of the other styles here as in four-styled flowers is also somewhat affected, but that seems to be the general rule. This is not so evident from figure 12. These observations on the styles, especially in the six- and seven-styled flowers, are of a preliminary nature. There seems then to be another axis of symmetry established in six-styled flowers, passing through *d*. This is similar in position to axes of symmetry in the flowers of *Impatiens glanduligera*, *Impatiens tricornis*, *Aesculus Hippocastanum*, *Urvillea*, *Serjania*, *Salvertia convallariodora*,

Vochysia oppugnata, *Qualea macropetala* and *Myoporum parvifolium* (Eichler, 1875, 1878). None of these axes established in the flower of *S. aquatica* with reference to missing and additional parts correspond with the axis of symmetry most usually occurring in flowers with a five-parted calyx, namely that passing through *b* and the center of the flower.

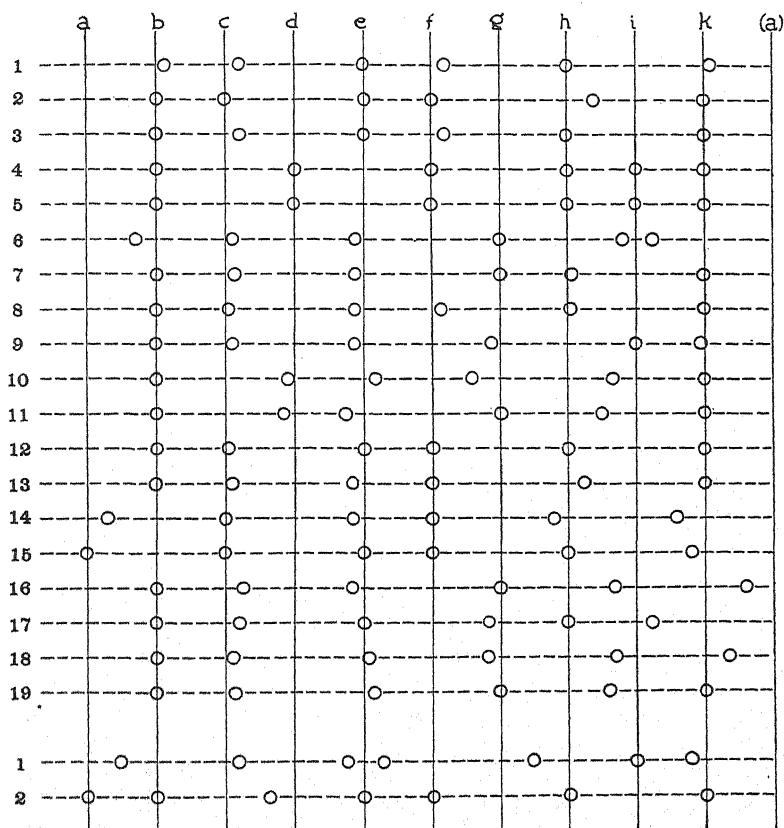
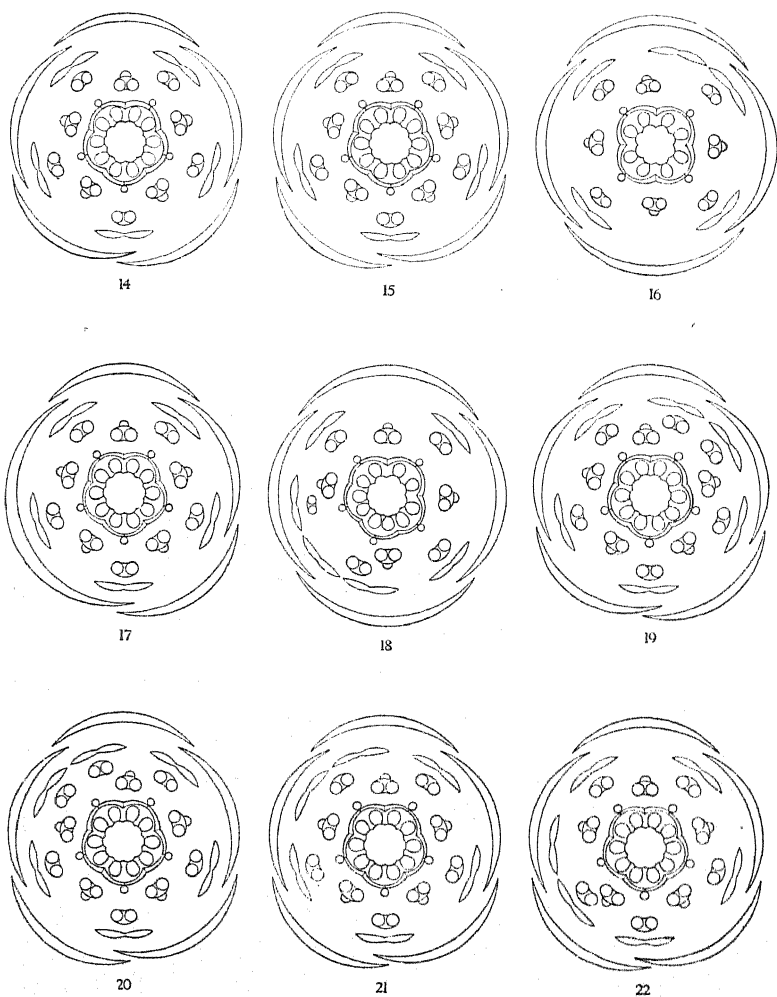
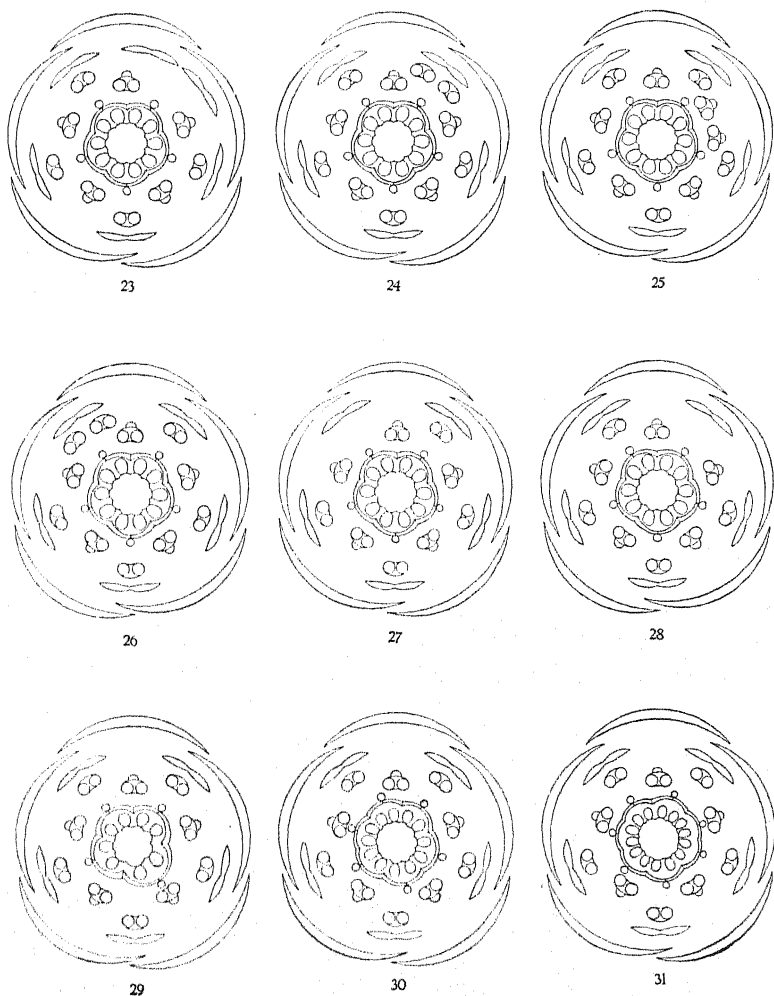


Fig. 13. Position of the styles in 19 six-styled flowers and 2 seven-styled flowers having the sepals overlapping as in figure 7.

The number of stigmas and styles is largely independent of that of the other organs. In only about one-fifth of the total number of flowers with other than five stigmas was one or more of the other whorls irregular. Since the variation in the number of carpels is greater than that of all the other parts



Figs. 14-22. Floral diagrams of *Stellaria aquatica*: 14, 15, typical flowers having the sepals overlapping as in figures 7 and 6 respectively; 16, 17, 18, flowers having four sepals; 19, 20, 21, 22, flowers having six petals, 19, 20, having eleven stamens.



Figs. 23-31. Floral diagrams of *Stellaria aquatica*: 23, a flower having six petals, nine stamens; 24, 25, 26, flowers having 11 stamens in various positions; 27, 28, flowers having nine stamens; 29, a flower having four carpels; 30, a flower having six carpels; 31, a flower having seven carpels.

combined it is evident that they must vary independently. There is a large number of possible combinations in the number of parts in the different whorls, and a great many occur. Flowers with four stigmas may have four, five, or six sepals; so also with the flowers having five stigmas. The number of stamens associated with these parts also varies. A few of the different and more common combinations are shown in figures 16-31. It is realized that here, as elsewhere in this work, mathematical and statistical treatment of the data might be offered, but it seems that that would add little to the general concepts presented.

Individual plants for purposes of flower study have not been grown; but flowers with varying numbers of parts have been observed in the same inflorescence; that is plants have not been found bearing flowers which have only four sepals, or four or six stigmas or eleven stamens etc. While it is possible that one plant may produce more flowers with four stigmas than another, no plants having only the atypical flowers have been found. This also applies to plants with imperfect flowers.

A glance at table 3 shows that the sepals manifest the least variation in number, the carpels the most, with the petals and stamens intermediate. The variability in the number of parts thus increases from the base of the floral axis toward the apex.

In addition to flowers with one or more stamens sterile, others have been observed in which not merely the stamens but the pistils as well are sterile. Such flowers show varying degrees of sterility and reduction, from those in which the petals, stamens and pistil are present but reduced in size, the stamens usually hard, dry, containing shrivelled pollen, the ovary wrinkled, tan or yellowish in color, supplied with minute ovules, to those extremely reduced flowers in which the corolla is apparently missing even when the flower is viewed with a binocular microscope, the stamens very small with little or no pollen, and the pistil very minute or practically failing to develop.

Stellaria aquatica shows two types of sterility, that in which the stamens are in part or wholly non-functional but the pistils produce seeds if pollination is effected, and that in which neither stamens nor pistils function. Flowers of the latter

type may be produced at various places in the inflorescence, the first flower sometimes being so modified. This represents a weakening of the dichotomous cyme (Parkin, 1914). These sterilities would be considered by Stout (1916) as sterility from impotence; in the one case partial impotence involving the stamens, and in the other complete impotence with reference to both kinds of sporophylls. According to the classification of Sirks (1917) there is partial unilateral sterility (of the stamens), total unilateral sterility (of the stamens), and total bilateral sterility (in which both stamens and pistils fail to function). Whether there is a partial and total unilateral sterility involving the pistils has not been determined. These types of sterility are found rather commonly in the angiosperms.

GENERAL CONSIDERATIONS AND DISCUSSION

From the data presented in the preceding pages it is evident that the variations in *S. aquatica* are governed, to an extent at least, as to their position in the flower; by the frequent occurrence of variations in definite positions, axes of symmetry are established, through position *h* with reference to additional petals, three-lobed petals, and additional stamens, through position *f* with reference to missing stamens, through position *a* in flowers having four stigmas, and through position *d* in flowers having six stigmas. These axes are shown in their relationships in figure 5b, the axis through position *h* being indicated with a solid line in each flower, that through *a* and *f* with a broken line, that through *d* with a dotted line. While it is true that the oblique directions of the internodes in the inflorescence cannot be shown in such a diagram, the bracts at the nodes are typically horizontal in the living condition, as are the flowers while they are open, so that except for the different levels in the inflorescence the diagram is representative of the relations as they actually exist. It remains still to be established however that all the axes of symmetry represented there can occur in each of the positions in the inflorescence; this has not been investigated in the present study. As a rule of course not more than one of the axes is established in the same flower. Comparing the two flowers which terminate the two branches originating at the same node in the inflorescence with the flower at that node it is evident that the axis through

f in flower number 2 in figure 5b forms an angle of 90° with the axis through *f* in flower number 1; the axes through *h* in these two flowers also form an angle of 90° , and those through *d* also form the same angle. On the other hand the axis through *f* in flower number 2' forms an angle of 162° with the axis through *f* in flower number 1, that through *h* in flower number 2' one of 18° , and that through *d* one of 54° with the similar axes in flower number 1 respectively. Similarly the axes of flower number 3 are at right angles respectively with those of flower number 2, while those of flower number 3' through *f*, *h*, and *d* again form angles of 162° , 18° , and 54° respectively with the similar axes of flower number 2. The axes of flowers number 3' and 2' are again at right angles, while those of flowers number 3 and 2' again form angles of 162° , 18° , and 54° . It may thus be said that of the two branches developing at a flowering node, that terminated by a flower having the sepals homodromic in origin with those of the flower at the node from which the branch develops will have these axes all at 90° with the similar axes of the flower at that original node; in the flower terminating the other branch these axes through positions *f*, *h*, and *d* will be at angles of 162° , 18° , and 54° respectively with the similar axes of the flower at that original node.

Axes *f*, *h*, and *d* in flower number 2 form angles of 108° , 108° , and 36° with the same axes in flower number 2'; this is true also for flowers 3 and 3', 4 and 4', etc., for flowers terminating branches which originate at the same node. It may then be further said that the axes through *f*, *h*, and *d* of the one of two flowers terminating the two branches originating at the same node in the inflorescence will form angles of 108° , 108° , and 36° with the same axes of the flower terminating the other branch. The *f* axes of flowers 1 and 3', 2 and 4', 2' and 4, 3 and 5', etc., form angles of 108° (or 72°); the *h* axes also form angles of 108° (or 72°); the *d* axes form angles of 36° (or 144°). It is thus possible to consider the relationship between these axes of symmetry even though their occurrence in the inflorescence may not be very frequent. The relationships will usually not be as diagrammatic as in the figure.

It is evident that there are fluctuating variations in *S. aquatica*. The general topic of fluctuating variations has re-

ceived its due share of pages in modern biological literature. Whether evolution is considered to be due to the accumulation of minor variations, or whether the key to the scheme of descent is sought in larger mutations, variations of a minor nature cannot be denied throughout the organic world; it is their interpretation that gives rise to disagreement. Morgan, Sturtevant, Muller, and Bridges (1922) assert that the effects of factors may be modified by 'environmental' and 'developmental' influences as well as by other factors. Morgan (1926) admits the possibility that the gene may be stable 'because it fluctuates quantitatively about a persistent standard', though he inclines to the view that 'the gene is constant because it represents an organic chemical entity.' The importance of the environment, especially as regards sexual relations in plants, has been strongly emphasized by Schaffner (1921, 1922, 1923a, b, 1926, 1927a, b, 1928) whose extended observations and experiments show that in certain plants at least, such as *Cannabis sativa*, *Arisaema triphyllum*, *Arisaema Dracontium*, *Humulus japonicus*, and *Zea Mays*, the important sexual relations may be modified by external influences.

Aside from the importance of variations from the evolutionary and genetic standpoints among others, they are of significance also in the concept of types. This concept is ancient; it goes back at least to Aristotle. With the development of systematic botany, especially by Linnaeus, the nomenclatorial type concept received a great impetus.

While the existence of forms in evolutionary relationship has been so universally admitted since Darwin's time, their boundaries, partly at least because of their variability, have been much disputed. The existence of races and varieties in many species cannot be questioned; and the study and establishment of such varieties can apparently go to great lengths. The present study, however, has not been in the nature of a genetic investigation; such researches are still to be done on *S. aquatica*. That lines could be established, 'pure' for various characteristics at least, seems possible. But these would still have much in common with the concept of *S. aquatica* presented in the preceding pages; and such work would make a previous general study of the plants as found in nature all the more fundamental.

Despite the great number of species, races, and varieties

described for many plants, the concept of biologic types which are the results of physical and chemical forces has not been strongly emphasized. For the lower plants Harper (1916, 1926) has put forth such factors as the angular relations of cells, mutual pressure, adhesion, surface tension, and inherited form tendencies; and again diminishing load and maximal resistance. Lewis (1923, 1925) has established the tetrakaidecahedron as the type for cells in certain tissues.

There has been an attempt in the preceding pages to disclose the type, if any be present, for the stem, the inflorescence, and the flower of *S. aquatica*. In any complete study of types not merely a single species but related forms as well should be investigated. The stem with leaves decussately arranged seems to be typical. Whether the symmetrical production of branches in a single or in a double spiral is to be considered the true type, or whether it is passing from one to the other is still an open question. To say with Thompson (1917) that phyllotaxy is due to the 'steady production of similar growing points, similarly situated, at similar intervals of time' is merely putting the problem one step farther back; and the 'laws' of cell division and growing points are intricate but not unquestioned.

The symmetry of the true dichotomous cyme suggests a real type, and the regular, pentamerous, symmetrical flower is a type in itself. Loss of parts apparently has been and is going on in the stem, the inflorescence and the flower. This may be the explanation of single and double spirals formed by the branches on the stem, especially since the condition of opposite leaves is looked upon as a derivation from an originally spiral type; it undoubtedly seems to be the explanation of the breaking down of portions of the cyme and the reduction in the floral parts. This too, it is realized is by no means an ultimate answer. Whether the production of supernumerary floral parts is a tendency toward type formation in a new direction, or a harking back to an original type with a larger number of floral parts cannot yet be regarded as settled; the latter is in agreement with accepted theories as to the origin of the Caryophyllaceae.

The physical and chemical bases of stability in the higher plants, aside from angular relations and patterns of symmetry are difficult to approach, and further interpretations are reserved for the accumulation of additional data.

In the preceding pages emphasis has been put upon variations as emphasizing the types. The results indicate that many of these minor differences not only in plants of the same species, but even in different parts of the same plant, are not merely haphazard, but in many cases definitely fixed. The ultimate explanation of the possibility of predicting in which position in these terminal, usually actinomorphic flowers certain irregularities will occur with reference to the sepals, and consequently with reference to the bracts, the inflorescence, and the branches of the stem, is still unknown.

SUMMARY

1. Primary stems of *Stellaria aquatica* have the branches, and branches in turn have the smaller branches upon them arranged either in a clockwise or in a counterclockwise spiral, and sometimes in a double spiral. Clockwise and counterclockwise spirals occur in approximately equal numbers. The same plant as a rule shows both types of spirals on different branches with no apparent regularity in their distribution. There may be apparent reversals in the direction of the spirals.

2. The cotyledonary node frequently has two branches in the axil of each leaf, and the two following nodes have as a rule one branch in the axil of each of the leaves.

3. As pointed out by the older authors, the overlapping of the sepals of the first flower is correlated with the arrangement of the branches; the position of the flower in the inflorescence is also correlated with the position and overlapping of the sepals and the direction of the bending of the pedicels as shown diagrammatically in figure 5b.

4. There is a decided variation in the number of parts in the flower, increasing from the base of the floral axis toward its apex, the sepals manifesting the least variation, the carpels the most. Additional petals and stamens, missing stamens and carpels, and probably additional carpels are fairly fixed as to the position in the flower in which they most frequently occur with reference to the sepals, and consequently with reference to the bracts and the position in the inflorescence. Thus axes of symmetry are established in the flower in definite relationship to similar axes in other flowers in the inflorescence.

5. There is a sterility of the stamens which shows a rather

gradual increase as the season progresses. Certain stamens are more frequently sterile than others. Some flowers show sterility of both stamens and pistils, such flowers being comparatively minute.

6. The type characteristic of the stem, the inflorescence, and the flower of *S. aquatica* is emphasized.

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¹¹ This paper, in which Desvaux anticipates modern tendencies in splitting genera, is not listed in the British Museum *Catalogue of Scientific Papers*, and appears to have been unknown to the compilers of the *Index Kewensis*. Even Pritzel indicates that volume 3 of Desvaux' *Journal de Botanique Appliquée* ended with page 192. Number 5 of that volume, consisting of pages 193-240 (for May, 1814), was evidently delayed in publication until after the appearance of volume 4: a footnote on page 197 shows that it was not published before February 1816. This number 5 is found in the file of the *Journal* recently acquired by The New York Botanical Garden from the Barnhart library. We are indebted to Dr. John Hendley Barnhart for bringing it to our notice.—T. E. H.

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Not *Piper angustifolium* Lamarck:
not *Piper elongatum* Vahl

WILLIAM TRELEASE

Ever since scientific names have been given to what are taken for species in nature as a means of intelligible reference to them, it has been recognized that one name cannot consistently designate more than one species. By common consent naturalists have come to retain a given name for the species to which it was given first, whenever through lack of information or through error it has been applied to several species. Though constituting no part of the name, an indication of the person who first published it is commonly appended to it; and pending its complete stabilization, it usually is followed by a negative indication of the same name, with similar author citation, in case others have used it to designate other species.

In 1791 Lamarck named a small Cayenne shrub *Piper angustifolium*. So far as known even yet, it occurs only in the Guianas and the lower Amazon region.

Seven years later, apparently in ignorance of Lamarck's publication, Ruiz and Pavon gave the same binomial, *Piper angustifolium*, to the narrower-leaved form of 'matico,' which is confined to the eastern slope of the Andes and is exported, for medicinal use, chiefly from Bolivia. Obviously, *Piper angustifolium* Ruiz and Pavon, not *Piper angustifolium* Lam., needed rechristening; and in 1805 it was renamed *Piper elongatum* by Vahl.

For some reason, possibly through similar oversight, Roxburgh in 1820 again used the same binomial, *Piper angustifolium*, for an entirely different Indian herb; and a decade later Dietrich entirely renamed this *Piper angustifolium* Roxb.,—not *P. angustifolium* Lam., not *P. angustifolium* Ruiz & Pav.,—*Peperomia Roxburghiana*, though he might possibly have done better by retaining the trivial name given by Roxburgh when making the new binomial, as was done by Casimir de Candolle subsequently, under a procedure now generally approved.

Quite paralleling the practice of fixing one binomial for each kind of plant, and an expression of the same effort to give unmistakable significance to names, there has arisen the common practice of bringing together for each species under its accepted name any different names which it may have received through

oversight or error. The elimination of such synonyms borne by a given species is of equal importance with the elimination of all but one species designated by a given homonym.

This conventional treatment of both synonyms and homonyms is essentially a matter of book-keeping, based on ascertained facts. Unfortunately fact and opinion are not always sharply separable in the interpretation of 'species,' and it is quite humanly possible to err either in considering two differently named forms to be specifically identical or in considering two identically named forms to be specifically separable. This is a very weak point in a mid-Victorian convention which considered a binomial duly relegated to synonymy as virtually non-existent and therefore fully applicable to any other species.

That the medicinal 'matico' continues to be spoken of commonly—and uniformly in pharmacal circles—as *Piper angustifolium* Ruiz and Pavon, results from a still prevalent belief that finality in human judgments is achievable. After the Piperaceae had been monographed in 1869 by Casimir de Candolle, such finality was accorded his judgments as those of the only competent authority on a large and most intricately difficult family of plants.

In this classic handling of the genus *Piper*, Lamarck's prior use of the specific name *angustifolium* was not recognized as displacing the more familiar homonym of Ruiz and Pavon, so that the binomial *Piper angustifolium* was adopted for the 'matico'—under it, as synonyms, being placed the name *Piper elongatum* Vahl and its later equivalents *Steffensia elongata* Kunth and *Artanthe elongata* Miquel, as well as *Piper purpurascens* Dietrich; while the monographer forecasts rather than declares the now evident conclusion that what he names *Piper salviaefolium* (*Artanthe salviaefolia* Miquel) is likewise of this species. Published mention of *Piper angustifolium* or *Piper elongatum* from that point on compels recognition that there is fallacy in supposing that affixing an author's name to a binomial at all necessarily shows what the author himself meant when he named a species, because it actually shows only what the later writer considered and intended the accepted name to stand for.

Up to this point, the synonymy of the 'matico' is free from error except that Vahl's binomial should have headed the

list and that the name used by Ruiz and Pavon should have replaced it in the list of synonymic discards. Unfortunately a graver error enters here, because the geographically localized 'matico'—which has deeply bullulate-lacunose leaves—was not distinguished from a somewhat similar Peruvian pepper with smoother leaves that Ruiz and Pavon themselves had named *Piper granulosum*; and either directly or as varieties this and several similar forms were made to extend the range of the amplified *P. angustifolium* as far afield as through Brazil to the east and Panama and Cuba to the north.

Fuller and better and more extensive collections now make it certain that these outlying forms and the Peruvian *P. granulosum* are not co-specific with *Piper elongatum* or *P. angustifolium* in the sense intended by Vahl or Ruiz and Pavon, and they are very different from *P. angustifolium* Lam. These plants constitute a natural group and resemble *P. elongatum* chiefly in having hooked or strongly curved aments. From one another they differ in geographic occurrence, but their morphologic differentials are not readily stated with positiveness in every case.

The prototype of these outlying 'angustifolium' or 'elongatum' forms is the Jamaican *Piper aduncum* Linnaeus (1753), under which some of them have been put as forms of late years and in which all should be included if they represent a single species. The next in priority is the Peruvian *Piper granulosum* Ruiz and Pavon (1798), followed successively by the Venezuelan *P. celtidifolium* Kunth (1815), the Mexican *P. multinervium* Martens and Galeotti (1843), and the Caribbean *P. subrectinerve* C. de Candolle (1902).

If these are to be kept apart, as in my present opinion they should be, *P. granulosum* Ruiz and Pavon is limited to the southern Andes; *P. celtidifolium* Kunth ranges from the Colombian-Venezuelan region through the Isthmus and as far north in Central America as Nicaragua; *P. multinervium* Martens and Galeotti continues the series from Salvador to Mexico; and *P. subrectinerve* C. DC. is the Caribbean representative of *P. aduncum* Linnaeus, which, when these are excluded, is confined to the Greater Antilles, where it is accompanied by a very hairy form, *P. Ossanun* (C. DC.) Trelease.

The vastly diversified countries embracing the extensive lowlands east of the Andes also have *aduncum*-like peppers, some of which have received separate names; but none of them is capable of affecting the designation of the more boreal forms, whether these be kept apart, merged into one, or united in part only.

Still another use of the binomial *Piper elongatum* presents other and different nomenclatorial difficulties. Under the then fully sanctioned practice of re-employing in a quite new sense a name which had been buried in synonymy, Monsieur de Candolle did not hesitate to make use in the Prodrômus of this discarded name for a Brazilian plant of the palmately nerved Enckea group (all of the other '*elongatum*' forms being pinnately nerved Artanthes).

Though Monsieur de Candolle's riper study, embodied in a 'Piperacearum Clavis' on which his latest years were spent and which was published after his death, was not cast in a form specifically showing such facts, he rehabilitates in the 'Clavis' the true *Piper angustifolium* (though an error of the indexer of the work ascribes the name to Ruiz and Pavon instead of Lamarck), and he properly takes up for the 'mático' Vahl's name *Piper elongatum*—though unfortunately in the complicated sense in which it was understood when called *angustifolium* in the Prodrômus sixty years ago.

Unfortunately, though his earlier re-employment of *elongatum* when the name was supposedly dead is set right in the 'Clavis' by renaming the Brazilian Enckea *Piper hexandrum*, the converse untenable rechristening of Lamarck's *angustifolium* as *Piper consanguineum* (the trivial name adopted from Kunth) escaped correction when the 'Clavis' was prepared. It may be added that the Cayenne component of *P. Schlechtendahlia* of the Prodrômus is a co-type of Lamarck's species.

The purpose of this short negative contribution is not to clear up with finality the nomenclature of all of the species which at one time or another have been called *Piper angustifolium* or *Piper elongatum*, but to present positively the fact that neither of these names is applicable to any known pepper occurring in the West Indies or on continental North America.

Notes on Fabaceae—XII

PER AXEL RYDBERG

ASTRAGALUS L.

The genus *Astragalus* dates back to Linnaeus' Species Plantarum, where the author adopted it from Tournefort and other older writers. In fact it dates back to the old Greeks, who used the name for some leguminous plant. The historical type is probably *Astragalus christianus*, but *A. Onobrychis* L. should be regarded as the nomenclatorial type according to the American Code. It should therefore be limited to species with a two-celled, more or less woody, bony, or leathery, and short and sessile pod. These requirements are fulfilled by the sections ONOBRYCHIDES, ULIGINOSI, MOLLISSIMI, and CHAETODONTES of Gray's, Watson's, and Jones' revisions of the genus. I have also included *A. lentiformis* and *A. Lemmonii*, though the pod is reflexed, rather thin-walled, and acute on both structures, and *A. Breweri*, which Gray placed in the section OROBOIDEI and Jones in his DIDYMOCARPI. In Europe and Asia, the genus, as so limited, is represented by numerous species.

1. MOLLISSIMI

1. *ASTRAGALUS GIGANTEUS* S. Wats. was described from fruiting specimens collected by Dr. Havard at Fort Davis, Texas. Sheldon changed the name to *A. texensis* on account of the earlier *A. alpinus giganteus*. M. E. Jones regards it as the same as *A. yaquianus* S. Wats., and his description applies mainly to this. In my mind the identification is not well established, for *A. giganteus* is described as having 5 to 10 pairs of villous-pubescent leaflets and *A. yaquianus* as having 10-21 pairs of appressed villous leaflets. The type specimen of the former is much more hairy than in *A. yaquianus*. Jones (Rev. *Astragalus* 234. 1923) makes the following statement: 'Pringle's No. 1218 distributed as a part of the type of *yaquianus* [*yaquianus*] is this species.' This is not quite correct, for the latter was wholly based on that number. Jones, notwithstanding, proposes a new variety, *A. giganteus* var. *yaquianus*, based on Watson's species as to the name, but the description applies to the next species. Jones also gives the distribution as extending to Guerrero. This is not, as it seems, the state of

Guerrero, but the type locality of *A. yaquianus* on the Yaqui River which was near the town of Guerrero, Chihuahua. It is related to *A. mollissimus*, but has better developed stems, ochroleucous flowers, nearly straight, abruptly acuminate, and broader pod. The following specimens belong to *A. yaquianus*:

CHIHUAHUA: Upper Yaqui River, *Pringle 1218*; Madera, *Palmer 295*.—NEW MEXICO: Lincoln County, *Wooton* in 1895; 3423 in 1907, 3960 in 1908; *Plummer 1903*; *Eggleston 14446, 14452*; White Mountains, *Wooton 327*; Gray's Peak, *Earle & Earle* in 1900; Ruidoso Creek, *Wooton* in 1895; Lincoln County, *Eggleston 14446*.—TEXAS: Upper Concho, *Reverchon 1281*; Fort Davis, *Havard*; *Ferris & Duncan 2543*.

2. *ASTRAGALUS HARTMANII* Rydb. See notes under the preceding species, from which this differs in the much larger flowers and large, thin, and less pubescent leaflets. It is known only from the type locality, San Diego Ranch, Chihuahua, *Hartman 678*.

3. *ASTRAGALUS MOLLISSIMUS* Torrey was described from specimens collected by James on the Platte River. Together with the two preceding, it differs from the rest of the species of the group by the glabrous pod. Jones made the following statement that the pod is 'inclined to be velvety pubescent when young,' which I think is wholly erroneous. In New Mexico the plant is often much smaller than on the plains, with smaller leaflets, flowers, and fruit (*A. simulans* Cockerell). Such specimens are:

NEW MEXICO: *Wright 367*; Las Vegas, *Cockerell* in 1901; Gray, *Skehan 7*; Roswell, *Tinsley*, in 1899; Union Co., *Standley 6122*.—TEXAS: Estelline, *Reverchon 4297*. The distribution of the species extends from Nebraska and Wyoming to Texas and New Mexico. Jones reported it from Flagstaff, Arizona, but I doubt the record.

4. *ASTRAGALUS ORTHANTHUS* A. Gray resembles *A. yaquianus* and *A. Hartmanii* in the more or less elongated stem, in the large flowers, and the straight banner, but the color of the flower is more red, or in one form white, the pod more rounded and densely pubescent.

VERACRUZ: Perote, *Halstead* (type).—NUEVO LEÓN: Saltillo, *Palmer 2137* (?).—PUEBLA: between Tinguattán and Cerro León, *Liebman 4683*.

5. *ASTRAGALUS SANGUINEUS* Rydb. It is related to *A. orthanthus*, but the plant is merely strigose, and the pod is larger and rounded at each end. The pod illustrated by Jones as *A. orthanthus* (Rev. *Astragalus* pl. 60, fig. 195) belongs to this species.

NUEVO LEÓN: Saltillo, in 1880, *E. Palmer* 243 (U. S. Nat. Herb. 43559).

6. *ASTRAGALUS HUMOLDTII* A. Gray was based on *Phaca mollis* H. B. K., the type of which came from Gasove, Valley of Mexico. Dr. Gray cited only one specimen that he had seen, viz. one in the Torrey Herbarium collected by Halstead, near the City of Mexico. Humboldt's specimens according to *Nova Genera et Species* were without fruit, and so is Halstead's, but both the original description of *P. mollis* and the plate, as well as Halstead's specimen, agree well with the species of southern Mexico, that is, with *A. Orizabae* Seaton, which name becomes a synonym. The plant of northern Mexico which has gone under the name of *A. Humboldtii* is quite different, and was until lately evidently without a published name. To *A. Humboldtii* belong the following specimens.

MEXICO (Federal District and State): *Humboldt*; *Halstead*; *Pringle* 7137, 11953; *Irola*, *Rose & Hough* 4557, in part.—VERACRUZ: *Orizaba*, *Seaton* 262; *Mueller* in 1855; *E. W. Nelson* 282.—PUEBLA: *Arsène* 1600; 7102; *Chalchicomula*, *Pringle* 8565; *Rose & Hay* 5663; *Esperanza*, *Pittier* 403; *Purpus* 3051.—HIDALGO: *Pachuca*, *Purpus* 401; *Rose*, *Painter & Rose* 8810; *Tequizquiac*, *Rose & Painter* 6635.—QUERETARO: Between *Cadereyta* and *Visaron*, *Rose*, *Painter & Rose* 9756; *Altamirano* 1645.

7. *ASTRAGALUS EARLEI* Greene. The first reference to this species may be found in *Biologia Centrali-Americana*, where Hemsley cites under *Astragalus Humboldtii* a specimen collected by Potts in Chihuahua, the true *A. Humboldtii* not being found in northern Mexico. The specimens distributed from there and so labelled belong mostly to the present species. It may be that Jones had derived his concept of *A. Humboldtii* from such specimens as *Pringle* 883, when he drew his description. The species is intermediate between *A. Bigelowii* and *A. Humboldtii*, perhaps nearer the former, differing in the more elongate, more curved pod, with much shorter hairs, the corolla also being smaller. As Jones cited no specimens, though

he gave a good description of this species, I adopted an unpublished name of Dr. Greene's and assign as the type *Earle & Tracy* (or *Tracy & Earle*¹) 226 as the type. Greene has also assigned another name to another number of the same collection.

TEXAS: Limpia Cañon, *Earle & Tracy* 226 (type, N. Y. Bot. Gard.); 237; 221; 276; Davis Mountains, 331; *Ferris & Duncan* 2661; Marfa, *H. C. Hanson* 389; Fort Davis, *Eggleston* 20201.—NEW MEXICO: Las Vegas, *Anect* 40.—CHIHUAHUA: Vicinity of the City, *Pringle* 189, 883; *Palmer* 5, and 78, in 1908; Parras, *Palmer* 242; Saltillo, *Palmer* 241.

8. *ASTRAGALUS IROLANUS* (M. E. Jones) Rydb. This is closely related to the preceding, differing mainly in the acute leaflets and the large flowers.

HIDALGO: Irola, *Rose & Hough* 4557, in part; (type)—MEXICO (State): Ixtapalapa, *Rose & Hay* 5641.

9. *ASTRAGALUS PERVELUTINUS* Rydb. The type was distributed as *A. Humboldtii*. It is related to it, but the pod is not so much inflated, slightly curved and more densely hairy. From *A. Earlei* it differs in the broader, less curved pod, and the larger flowers, and from both in the short tangled pubescence of the leaves, the broader leaflets densely covered with short tangled hairs.

CHIHUAHUA: City of Chihuahua, *Pringle* 189 (type in herb. N. Y. Bot. Gard.)—DURANGO: Tepehuanes, *Palmer* 14.

10. *ASTRAGALUS BIGELOWII* A. Gray is closely related to *A. mollissimus*, but differs mainly in the densely pubescent, broader and shorter, less arcuate fruit. The pubescence is also usually looser and the leaflets more round. It is distributed from Texas to Arizona, Durango, and San Luis Potosí.

11. *ASTRAGALUS THOMPSONAE* S. Wats. was described from specimens collected by Mrs. Thompson in southern Utah and named for her. Sheldon changed the name to *Astragalus syrticolus* on account of the older *A. Thompsonianus* Benth. Jones regarded it as a variety of *A. Bigelowii*, but it is readily distinguished by the white, short, and more spreading pubescence, the lax recemes, and the larger and different pod. It is common in eastern and southern Utah; it has also been collected elsewhere, namely:

¹ It has been distributed both ways.

ARIZONA: Deadman Ranger Station, Coconino County, *Eggleston 17189*; Moki Reservation, *Hough 56*.—NEW MEXICO: Aztec, *Baker 405*.—COLORADO: Westwater, *Jones*, in 1891; Mesa County, *H. C. Long*, in 1893.

12. *ASTRAGALUS MATTHEWSII* S. Wats. is related to *A. Bigelowii* and *A. Thompsonae*, but differs from the former in the white pubescence, the larger, less arcuate, more inflated and more long-hairy pod, the upper suture of which is almost straight, and from the latter in the more appressed pubescence and the less curved pod. It is known only from the type collection, from Fort Wingate, New Mexico, by Dr. Matthews, and by Dr. Palmer without locality.

13. *ASTRAGALUS MOGOLLONICUS* Greene is also related to *A. Bigelowii* and by Jones regarded as identical with it. The type, however, is covered with a long, brown, spreading pubescence, the raceme is nearly capitate and very dense, the leaflets suborbicular and the pod, sent later by Dr. Greene, is very small, about 1 cm. long, 5 mm. broad and deep, white-villous, scarcely sulcate on either suture and straight on the upper. It is known only from the type collection, Mogollon Mountains, New Mexico.

14. *ASTRAGALUS MARCIDUS* Greene is related to *A. Bigelowii* but the flowers are much smaller, the pod smaller and nearly straight on the upper suture.

TEXAS: Davis Mountains, *Tracy & Earle 319* (type); Marfa, *C. B. Greene* in 1895.—CHIHUAHUA: San Diego, *Hartman 605*.—COAHUILA: Aqua Nueva, Saltillo, *Palmer 559*.

15. *ASTRAGALUS ANISUS* M. E. Jones. This was collected near Pueblo, Colorado, by Miss A. P. Lansing in 1888, and evidently has never been collected since. It is not closely related to the other species of the group, differing from the rest in the small size, the appressed silky pubescence, the comparatively small flowers, and in the pod, which is more rounded, merely mucronate, more inflated, and with short appressed pubescence. Only *A. Matthewsii* approaches it in the pubescence of the leaves, and *A. Humboldtii* in the shape of the pod. In the National Herbarium there is a specimen somewhat similar without collector's name. The only original record given is 'Camp 82-83 April 28.' Dr. Gray has written on the label 'Apparently *Astragalus succumbens* Dougl.,' which evidently is wrong.

2. ULIGINOSI

16. *ASTRAGALUS CAROLINIANUS* L. This species was based on a description and plate in Dillenius' *Hortus Elthalmensis*. Most botanists have regarded this as the same as *A. canadensis* L., and the name has place priority on the page. Dillenius' plate resembles more the common plant here regarded as *A. canadensis*. Appended to his description, however, there appeared a comparison between *A. carolinianus* and another species on which Linnaeus based his *A. canadensis*. The only clue on which to base the identification of the latter is given in the description of the leaflets, which are said to be subcanescent beneath. This could only apply to the northern and more common plant, for in the southern plant the leaflets are sparingly and minutely strigose beneath. In the figure the calyx teeth are illustrated as very short, while in fact they are in *A. carolinianus*, as here understood, longer than those of *A. canadensis*, but this may have depended on the inaccuracy of the artist. As there are two closely related plants in eastern United States, and the northern one has the leaves subcanescent beneath, it may be well to retain the name *A. canadensis* L. for this, and reserve the name *A. carolinianus* L. for the southern. Jones regarded the latter a variety of the former, but his description of the pod 'decidedly inflated' is erroneous, for the pods are alike in both species, being oblong, not sulcate, and perfectly glabrous. Perhaps he confused it with *Phaca neglecta*.

MARYLAND: Cumberland, *Schrivver* in 1874.—VIRGINIA: Bushy Mountain, Smyth County, *Small* in 1892; Luray, *Steele & Steele* 46; Wytheville, *Shriver* in 1874.—WEST VIRGINIA: Hinton, *Millspaugh* 1146; White Sulphur Springs, *A. Brown* in 1892.—NORTH CAROLINA: Table Rock, *Heller* 32; Great Smoky Mountains, *Beardslee & Kofoid* in 1891; Yellow Hill, Swain Co., and Balsam Mountain, *Hulst* in 1882.—GEORGIA: Tugalo River near its junction with Seneca, *Gibbs* in 1855.

17. *ASTRAGALUS CANADENSIS* L. See notes under the preceding species. This is the most widely distributed species of *Astragalus* in North America, its range extending from Quebec to Hudson Bay, Alberta, Utah, Colorado, Oklahoma, and Virginia. There is also a record from Kettle River, British Columbia, *Macoun* 63754 and one from Dallas, Texas, *Reverchon*.

18. *ASTRAGALUS HALEI* Rydb. The type was collected in Louisiana, *Dr. Hale 313* (Torrey Herbarium, flowers); also at Shreveport, *Cocks 3624* (fruit). It is closely related to *A. carolinianus* but has about half as long calyx-teeth, and spreading fruit.

19. *ASTRAGALUS OREOPHILUS* Rydb. The type of this species came from Pagosa Spring, Colorado. It is intermediate between *A. canadensis* L. and *A. spicatus* Nutt., differs from the former in the usually broader leaflets, the broader and shorter bracts, the flowers more resembling *A. spicatus* and the plumper pod, and from the latter in the glabrous, less coriaceous pod and the narrow upper calyx-lobes.

COLORADO: Walsenberg, *Shear 4769*; Pagosa Springs, *Baker 419* (type); Trimble Springs near Durango, *Baker, Earle, & Tracy 478*; Wahatoya Creek, *Rydb. & Vreeland 5990*; Larimer County, *Osterhout* in 1897; Boulder, *Tweedy 5154*; Fort Collins, *Crandall* in 1898.—NEW MEXICO: Pecos River National Forest, *Standley 4377*; Colfax, *14656, 13861*; El Vado, Chama River, *Eggleston 5988*; Chama, *Standley 6546*.

20. *ASTRAGALUS MORTONI* Nutt. The type was collected by Wyeth on the sources of the Missouri. In the isotype in the Torrey Herbarium the specimen in flower has a decidedly black-hairy calyx, and bracts and the ovary is described as villous. Nuttall described the flowers as ochroleucous. Torrey and Gray placed it among the purple-flowered species, between *A. adsurgens* and *A. striatus*, not noticing that the relationship was to *A. canadensis* L., and *A. spicatus* Nutt. Watson made it a variety of *A. canadensis*. Neither Watson nor Jones have noticed that *A. Mortoni* has more or less black-hairy calyx and bracts, nor does the latter make any reference to the fact that the pod in *A. Mortoni* is pubescent and sulcate on the lower suture. In *A. canadensis* it is glabrous and without a sulcus. Both authors confused it with *A. spicatus* Nutt., which has white-hairy calyx. Whether the color of the hairs is of any value is perhaps questionable, but the black-hairy plant seems to be limited to the northwest, west of the continental divide, while the white hairy form is confined to the Rocky Mountains, on the western slope of which their ranges, however, overlap. In the white-hairy plant the pod is less turgid, the upper calyx-lobes are always twice as broad as the rest, and the bracts

broad and short. In the true *A. Mortoni*, the bracts and even the calyx-lobes approach more those of *A. canadensis*, but are shorter, and the pod less hairy and with a straighter beak than in the white-hairy plant, and sometimes glabrate in age. It is confined to the Pacific slope and widely distributed in Washington, Oregon, Idaho, northern California, and western Montana. It has been collected east of the Rocky Mountains at the following stations.

MONTANA: Helena, *Butler* 104, 1042; Gannet, *Mrs. Scheuber* in 1901.
—WYOMING: Gros Ventre River, *Merrill & Wilcox* 994.

21. *ASTRAGALUS PACHYSTACHYS* Rydb. This species was based on *Astragalus spicatus* Nutt.; not *A. spicatus* Pallas. See notes under *A. Mortoni*. Both Watson and Jones included this in *A. canadensis Mortoni*. The type came from the Rocky Mountains, most likely Wyoming. *Astragalus tristis* Nutt., which has also been regarded as a synonym of *A. Mortoni*, might seem to belong here, as the type locality was 'Rocky Mountains, towards the sources of the Platte,' hence Wyoming, but the calyx is described as being black-hairy. The species is unknown to me, as no specimens have been seen. *A. pachystachys* is common in the Rocky Mountains of Montana and Wyoming, especially east of the divide. Besides, the following specimens, found outside of the range proper may be included in it.

IDAHO: Tikura, Blaine County, *Nelson & Macbride* 1293; Bear Lake County, 1617; Blackfoot, *Mulford*; Lake Waha, *Heller* 3089; Latah Co., *Sandberg*; Pocatello, *Mrs. Soth* 544.—WASHINGTON: *Vasey* 275; Wilson Creek, *Lake & Hull* 667; Simcoe Valley, *Lyall*; Egbert Spring, *Sandberg & Leiberger*; Brickelton, *Suksdorf* 2268; Newman Lake, 8803.—BRITISH COLUMBIA: Lake Osoyoos, *Macoun* 70438.—NEVADA: East Humboldt Mountains, *Heller* 9204; *Watson* 261, in part.—SOUTH DAKOTA: Black Hills, *Forwood*; *Murdoch*.

22. *ASTRAGALUS TORREYI* Rydb. The plant was first collected by Torrey and in the same year by Stretch. The latter specimen was named by Torrey as *A. adsurgens*. So were also Kennedy's specimens. *Heller* 9465 and 9822 bore the name *A. nitidus*, which practically meant the same. I suppose that this misidentification depended on the fact that the leaflets are decidedly pubescent on the upper surface. The rest were

named *A. Mortonii*, but the calyx is not black-hairy and the pod is more like that of *A. pachystachys*, of which it may only be a form; the leaflets, however, are narrower, the flowers smaller, the calyx-lobes shorter, and the bracts and even the stipules narrower.

NEVADA: Empire City, Nevada, in 1865, *Torrey* (type, herb. Columbia University and N. Y. Bot. Gard.); Ruby Valley near Cave Creek Post Office, *Heller* 9465; Carson City, *Jones* 3843; Pleasant Valley, *Stretch* in 1865; Lake Tahoe, *Kennedy* 966; Carson, *Steinmetz* A.—CALIFORNIA: Lake Tahoe. *Leiberg* 5328; Truckee, *Sonne* in 1888; Mono Lake, *Congdon*.—IDAHO: *Henderson* 3298.

The following may also be referred here, though the leaves are only slightly pubescent above when young.

NEVADA: Carson City, *Heller* 9822; *Baker* 1063.—CALIFORNIA: Truckee, *Heller* 7035; Summit, 12904.

23. *ASTRAGALUS OREGANUS* Nutt. The type came from the 'plains of the Rocky Mountain range towards the sources of the Oregon,' i.e. somewhere in Wyoming or Idaho. The species was described from specimens in flowers only, and the plant was practically lost. *Torrey* and *Gray* placed it near to *A. flavus*, probably on account of its ochroleucous flowers and connate stipules. *Gray* retained it in the same place, including it in his *Ocreati*. When it was rediscovered by *Parry* on the *Jones'* Expedition to the Yellowstone Park, *Gray* and *Watson* did not recognize it, but it was redescribed as *A. ventorum* and placed in the section *ONOBRYCHIDES*, also known as *HYPOGLOTTIDES*. *Jones* has transferred it to the *ULIGINOSI*, which somewhat improved the matter, but it is not very closely related to *A. canadensis* and its relatives, and perhaps should constitute a section by itself. The only specimens in fruit seen by me are *A. Nelson* 9427 collected in 1910.

WYOMING: Tough Creek, *Aven Nelson* 9427; Steamboat Mountain, Sweetwater County, 7051; Point of Rocks, *Merrill & Wilcox* 731.—IDAHO or WYOMING: *Nuttall* (type).

3. HYPOGLOTTIDES

24. *ASTRAGALUS STRIATUS* Nutt. This was published in *Torrey* and *Gray's Flora* and was based on *A. Laxmanni* of *Nuttall's, Genera*, the type of which came from 'the hills of Missouri', probably South Dakota. *A. adsurgens robustior*

Hooker is also cited as a synonym, though Nuttall, both in the Genera and in Torrey & Gray's *Flora*, describes the calyx as 'blackish and puberulent' or as 'clothed with short black hairs,' while Hooker describes his variety as white-pilose, with very few black hairs. Hooker called the black-hairy form *A. adsurgens*, confusing it with the Asiatic species. Jones has adopted the name *A. nitidus* Douglas for this species, citing Hooker's *Flora* (1:149. 1834) as the place of publication, a nomenclatorial absurdity, which can not be admitted. For the first, *A. nitidus* Dougl. is not published, merely cited as a synonym of *A. adsurgens robustior*, not of *A. adsurgens* as understood by Hooker. The citation of a manuscript name as a synonym is not publication, either under the American or the International Code, and the name was applied by Jones to the wrong form. In the Torrey Herbarium there are two sheets received from Hooker. One of these sheets is labelled: '*Astragalus adsurgens*, Pall. Ex herb Hook. Saskatchewan, Douglas.' This represents the ordinary small plant having the calyx with rather numerous short black hairs. The other sheet bears only '*A. adsurgens* β Hook.' without any indication of collector or locality. This sheet contains two larger specimens on which the calyx is almost destitute of black hairs. If this sheet represents *A. adsurgens* β Hook., it is an isotype of *A. nitidus* Dougl. It is, however, not exactly *A. striatus*, for that is the more or less black-hairy common form, usually known in this country as *A. adsurgens*. Neither is it *A. sulphurescens* Rydb., nor *A. Chandonnetii* Lunell, which Jones also cited as synonyms of the variety. *A. striatus* Nutt. is so common in the Rocky Mountain region that no specimens need to be cited.

In regard to *A. nitidus robustior* M. E. Jones (Rev. *Astragalus* 170. 1923) it may be said, that it is a great mixture of facts and errors. It is based on *A. adsurgens robustior* Hooker with *A. striatus* Nutt., *A. sulphurescens* Rydb., and *A. Chandonnetii* Lunell given as synonyms, and the following description: 'Flowers white in short heads, on elongated peduncles. Calyx teeth long.' As stated before, *A. adsurgens robustior* is the basis of *A. nitidus*. *A. striatus* Nutt. is the same as *A. adsurgens* Hook. or *A. nitidus* as understood by Jones, but not of Hooker. 'Flowers white' agrees with the description of *A. Chandonnetii*,

scarcely with that of *A. sulphurescens*, and certainly not with either var. *robustior* Hook. or *A. striatus* Nutt. 'Short heads on elongated peduncles' applies to all, at least in flowering stage; 'calyx-teeth long' only to *A. sulphurescens*.

Astragalus terminalis Wats. in the original publication was said to be related to '*A. adsurgens*,' i.e. *A. striatus* Nutt. It being at that time practically unknown to me, I included it in the HYPOGLOTTIDES in my *Flora of the Rocky Mountains*. Jones has shown its relationship to his own *A. revertoides*, making the latter a variety of the former. I think that they are identical, and that Watson committed an error in describing the corolla as purplish, while in reality it is cream-colored with the keel purple-tipped.

25. *ASTRAGALUS CHANDONNETII* Lunell. This was first described as *A. adsurgens albiflorus* in 1905 by Blankinship from Montana. As there is an *A. albiflorus* Gand. 1902, the later name of Lunell's has to be adopted. *A. Chandonnetii* differs from *A. striatus* not only in the color of the corolla (rather cream-colored than white as described), but also in the foliage which is densely silky strigose on both sides. In my *Flora of the Rocky Mountains* it was included in the next species.

MINNESOTA: McHugh, near Detroit, *Chandonnetii*.—MONTANA: Mount Helena, *Butler* 1080; Mount Ascension, 881, 4079, 1082; Prickly Pear Valley, 4111; Deer Lodge, *Rydberg* 2699; Helena, *Kelsey* in 1892; Belt River, *F. W. Anderson* in 1883; *Safford* 557.—WYOMING: Gillette, *E. V. Wilcox* 429; Slater, *Goodding* 1737.

26. *ASTRAGALUS SULPHURESCENS* Rydb. was described in 1901 from specimens from Georgetown, Colorado. It differs from *A. striatus* in the ochroleucous corolla and the longer calyx-lobes, and from *A. Chandonnetii* in the longer calyx-lobes, the more or less black-hairy calyx and pod, and the glabrous or glabrate upper surface of the leaves. It was redescribed the following year by Gandoger under the name *A. Crandallii*. It is confined to the mountains of Colorado.

COLORADO: Along Platte River, *Jones* 851; Boulder Cañon, *Penard* 184; Boulder, *Hanson* in 1920; Georgetown, *Rydberg* in 1895; *Shear* 4509; Estes Park, *Osterhout* in 1895, and 2806, 1903; Boulder, *Tweedy* 5152; *Vestal* in 1913; Empire, 5641; Como, *Crandall* 90; *Crandall & Cowen* 128; Clear Creek,

Patterson 18; Eldorado Springs, *Clokey 2809*; Boulder County, *C. P. Smith 3147*; Headwaters of Clear Creek, *Hall & Harbor 136*.—WYOMING: West of Cheyenne, *Morris* in 1901.

27. *ASTRAGALUS BREVIDENS* Rydb. The type was collected 3 miles north of Whitney, Baker County, Oregon, Febr. 22, 1921., *M. Peck 10360*. The specimens were labeled *Astragalus Mortoni* Nutt., to which it has only superficial resemblance. It is evidently related to *A. Chandonnetii*, but differs in the broader leaflets, glabrous above, the short-villous instead of strigose pubescence on the calyx and pod, and the short calyx-teeth.

28. *ASTRAGALUS GONIATUS* Nutt. This was apparently first collected by Richardson and then certainly by Drummond and referred to the European *A. hypoglottis*. The American plant was first recognized as distinct in Torrey & Gray's *Flora*, where it was published as *A. hypoglottis polyspermus* (T. & G. Fl. N. Am. 1: 328. 1838). On the second page following, it was redescribed as *A. goniatus* Nutt.; neither Nuttall, nor Torrey and Gray noted that they were the same species. Jones (Proc. Calif. Acad. II. 5: 646. 1895), adopting the name *A. agrestis* Dougl., made the same error as he did in adopting *A. nitidus* Dougl., in applying Douglas' manuscript name, cited as a synonym under the variety β , to the species itself. *A. agrestis* in Hooker's *Flora* appears only as a synonym and therefore was not published. Furthermore *A. hypoglottis* of Hooker's *Flora*, of which *A. agrestis* Dougl. is a synonym, is not the plant described by Jones, but a closely related plant with pale calyx, practically devoid of black hairs, long calyx-teeth, about as long as the tube and larger corollas. Douglas' type, or at least an isotype of the same, was seen by me, when visiting Kew and the British Museum in 1901. *A. goniatus* is common in the Rocky Mountain region, extending into eastern Washington and Oregon, and in the northern Sierra Nevada. The following specimens have been collected on the eastern plains.

NEBRASKA: Gordon, *Bates 582*.—SOUTH DAKOTA: Sheep Mountains, *Visher 2391*; Brookings, *T. A. Williams*; Daland, Spink County, *Carter* in 1897; Upper Missouri, *Nicollet*.—NORTH DAKOTA: Leeds, *Lunell* in 1902-6. —MINNESOTA: Fish Lake, *Chandonneti*; Fergus Falls, *Sheldon* in 1892. —MANITOBA: Portage la Prairie, *Macoun & Herriot 70492*.

29. *ASTRAGALUS VIRGULTULUS* Sheldon was described in 1894 from specimens from Boulder, Colorado, collected by Patterson. It was also noted by Prof. Aven Nelson in his First Report on the Flora of Wyoming without a name, but was distributed as *A. hypoglottis ochroleucus*. Later it was described by Osterhout as *A. hypoglottis bracteatus*. Jones (Proc. Calif. Acad. II. 5: 647. 1895) first stated that '*A. virgultulus* is the same as *A. agrestis* apparently;' later (Contr. W. Bot. 10: 65. 1902) as *A. agrestis polyspermus* M. E. Jones, based on *A. hypoglottis polyspermus* T. & G., and at last (Rev. Astragalus 171. 1922) the same, adding that it 'is the form growing unsupported by other plants in more exposed places and is ashy-puberulent with pods 7 mm. long and short internodes.' Sheldon describes it as having ochroleucous flowers, leaflets glabrous above with scattered hairs beneath, calyx-tube slightly pubescent with white hairs, calyx-lobes equalling the tube in length, and pod 10-12 mm. *A. hypoglottis polyspermus* was described as dwarfish and much branched, somewhat decumbent, pubescent, calyx longer than the bracts, very hirsute, the hairs partly black, the teeth scarcely half as long as the tube. As no mention is made of the color of the flower, it is presumed that the color was as described under *A. hypoglottis* i.e. bright purple. In the Nuttallian specimens in the Torrey Herbarium they evidently had been so in the fresh state. Do these descriptions agree? Can any one rely on such statements of identification made by Jones? Sheldon did not describe the large bracts, noticed by Osterhout, but he described the large stipules, which usually accompany the large bracts in this species.

COLORADO: Boulder, *Patterson*.—WYOMING: Laramie River near Colorado Line, *Osterhout* in 1896 and in 1898; Meadow Creek, *A. Nelson* 775; Bitter Creek, 4783; Elk Mountains 4091.

30. *ASTRAGALUS TARLETONIS* Rydberg is also related to *A. goniatus*, but has larger flowers, rather fleshy bracts, and long calyx-teeth as *A. agrestis*, but the calyx is strongly black-hairy. The type came from Five Finger Rapids, Yukon. In the Torrey Herbarium there is a specimen from arctic America sent by Dr. Hooker, but without locality or collector. This might have been collected by Richardson. Two specimens

similar to that in the Torrey herbarium were found at the Philadelphia Academy. These came through Short's herbarium and are labeled 'Astragalus Hypoglottis, Frankl. Exp. W. J. Hooker, LL. D.' One of these has been donated to our herbarium. Richardson's specimens, recorded as *A. hypoglottis* came, however, from the Saskatchewan River. Besides these, I have seen one from Fifty-mile River, Alaska, collected by Bolton in 1899.

31. *ASTRAGALUS AGRESTIS* Dougl. As stated above, this name appeared first as a synonym under Hooker's *A. hypoglottis*, the type of which came from the fertile plains of the Red River, Manitoba. See notes under *A. goniatus*. The plant is larger than *A. goniatus* usually is, with larger corolla, pale calyx and long calyx-lobes, and usually longer leaflets. The only similar specimens seen are the following.

MONTANA: St. Ignatius Mission, *MacDougal* 298.

4. CHAETODONTES

This group was established by Dr. Gray, and based on *A. Spaldingii* (originally described as *A. Chaetodon* Torr.) and *A. Lyallii* A. Gray. Later *A. Austiniae* A. Gray was added. Jones in his *Astragalus* included also *A. Brauntoni* Parish, which, however, is not related to the rest. *A. Lyallii*, though somewhat similar in habit to *A. Spaldingii*, has a flattened thin-walled, reflexed pod, which all indicate its relationship to *A. lentiformis* A. Gray and *A. Lemmoni* A. Gray; it has also the small corolla of these species.

32. *ASTRAGALUS SPALDINGII* A. Gray was originally described as *A. Chaetodon* Torr. As that name had already been used by Bunge, Gray changed it to the present one. It is fairly well understood; its range comprises Washington, Oregon, and western Idaho.

33. *ASTRAGALUS AUSTINAE* A. Gray was described from specimens collected by Lemmon on Mount Stanford (Castle Peak), Nevada County, California. It is closely related to the preceding but has somewhat the general habit of *Hamosa Andersonii*.

CALIFORNIA: Castle Peak, *Leiberg* 5297; *Jones* in 1902; *Smiley* 480; *Lemmon* 71; Placer County, *Sonne* 673; also in 1892.—NEVADA: Mt. Rose, *Heller* 9936.

5. LENTIFORMES

This group is characterized by the small flowers, small, thin-walled, elliptic or lanceolate pod, decidedly flattened, with the upper suture acute, and the sulcus on the lower suture, if any, very narrow. The group is included in *Astragalus* with some hesitation.

34. *ASTRAGALUS LYALLII* A. Gray was described from specimens collected by Lyall on the Upper Yakima, Washington. It has always been associated with *A. Spaldingii*, but I think it is more closely related to *A. Lemmonii* and *A. lentiformis*. See remarks under *CHAETODONTES* above.

WASHINGTON: *Whited* 343; 97; *Vasey* 274; Upper Yakima, *Lyall* 8; *Henderson* 2354; *Suksdorf* 1816; Walla Walla, *Wilkes Expedition* 543; *Brandegee* 717; North Branch of the Columbia, *Wilkes Expedition* 543a; *Ellenburg, Piper* 2683; *Elmer* 366; Morgan's Ferry, *Suksdorf* 282; Ainsworth, *Tweedy* 6151. —IDAHO: Twin Falls County, *Nelson & Macbride* 1713; Elmore County, 1020; Glen's Ferry, *Jones* in 1911 (luxuriant form with large fruit; var. *caricinus* M. E. Jones).

35. *ASTRAGALUS LENTIFORMIS* A. Gray was described from specimens collected by Lemmon in Clover Valley, Sierra Nevada. This species is remarkable on account of its thick woody caudex, and sparse villous pubescence. Jones referred this, as well as the next, to the *MICRANTHI*. As I have stated in another place, Gray's *MICRANTHI* was based mainly on *A. Nuttallii* and its relatives, and should properly belong to what Jones called *LEPTOCARPI*. Jones' *MICRANTHI* consists mostly of Mexican species, not closely related to *A. lentiformis* and *A. Lemmoni*.

CALIFORNIA: Sierra County, *Lemmon* 50, in part, 73; 537.

36. *ASTRAGALUS LEMMONI* A. Gray was also described from specimens collected by Lemmon in Sierra County, California, and is closely related to the preceding, but has shorter stems.

CALIFORNIA: Northern California, *Webber, Lemmon*; Sierra County, *Eastwood* 7791; *Lemmon* 50, in part, 72, 187; Kanix Reservation, *Austin & Bruce* in 1897; Siskiyou County, *Greene* in 1876; Chat, *Jones* in 1897. —OREGON: Farwell's Bend, Crook County, *Leiberg* 454.

37. *ASTRAGALUS PECKII* Piper. This species is related to *A. Lemmoni*, differing mainly in the lower habit, and smaller

acute leaflets. Cusick's specimens were labelled *A. lentiformis* and probably were included by Jones in that species, as he cites specimens from Crook County, Oregon. The species is closer to *A. Lemmoni* than *A. lentiformis*.

OREGON: Crook County, *Peck* 9768; *Cusick* 2818.

6. BREWERIANI

38. *ASTRAGALUS BREWERI* A. Gray has no close relative in America, nor as far as I can find, in the Old World. The plant is annual and has some resemblance to *Hamosa tenera* and its allies, but the pod is different, coriaceous, erect, deeply sulcate on the lower suture, and with a stout beak as long as the body itself. The fruit resembles that of *A. Onobrychis* L. of Europe, but its general habit does not. Dr. Gray, who had no mature fruit, placed it next to *A. tener*. Jones transferred it to the DIDYMOCARPI, i.e., the genus *Hesperastragalus* Heller, with which it has no relationship.

CALIFORNIA: Tamalpais, *Brandegee* in 1891; *Eastwood* 3164; Mendocino County, *Abrams* 7018; *Rattan* in 1884; Sonoma County, *Heller & Brown* 5218 in 1902; *Brewer* 979 (type); Lake County, *J. P. Tracy* 1647; *Curran* in 1884; Marine County, *Brewer* 955.

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE 1927-1929

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